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Soil-Woodland Correlation in Northern Idaho[1]

Approximately two-fifths of Idaho's land is forested (Wilson, 1962). More than 25 million acres need to be restored or improved (Idaho Conservation Needs Committee, 1963). Often it is difficult to recommend specific tree species for reforestation because of the absence of adapted trees by which to measure potential site quality.

Through soil-woodland correlation, site quality may be estimated by identifying the soil in question and relating it to similar soils of known productive capacities. The objective of this study was to formulate regression equations from previously collected data to predict site quality in areas which have been burned or otherwise disturbed.

Methods

Over the past 14 years data from over 200 plots in northern Idaho have been collected by a team consisting of a soil scientist and woodland specialist of the Soil Conservation Service. Each plot represents a soil series with a normally stocked overstory of measurable trees.

The soil scientist described the soil profile in accordance with standard nomenclature (Soil Survey Staff, 1951). The woodland specialist recorded height and age of four to five dominant and/or codominant trees, stand density, and composition of both overstory and understory. These data were used in this study.

One hundred forty-four plots (Fig. 1) were eventually selected: 47 plots of ponderosa pine (*Pinus ponderosa*), 24 plots of lodgepole pine (*Pinus contorta*), 25 plots of western white pine (*Pinus monticola*), and 48 plots of western larch (*Larix occidentalis*). The soil profile at each plot was classified in accordance with the Soil Survey Staff (1967). Site index was computed based on tables by Meyer (1938), British Columbia Forest Service (1947), Haig (1932), and Cummings (1937).

Regression analyses were used. Since much of the data was discrete (discontinuous), a choice had to be made; either the data must be split so that discrete variables in one half could be coded and used in regression to test the other half, or the authors' knowledge of the area must be relied on to establish codes for the discrete data to test the entire 144 plots. Splitting the data would result in increasing sampling error. The results of using data coded by the authors would, in part, be a reflection of the authors' knowledge

[1] Idaho Agr. Exp. Sta. Research Paper No. 826. Contribution from the Department of Agricultural Biochemistry and Soils, University of Idaho. Portion of an M.S. Thesis of Senior Author, University of Idaho, Moscow, Idaho. 1969.

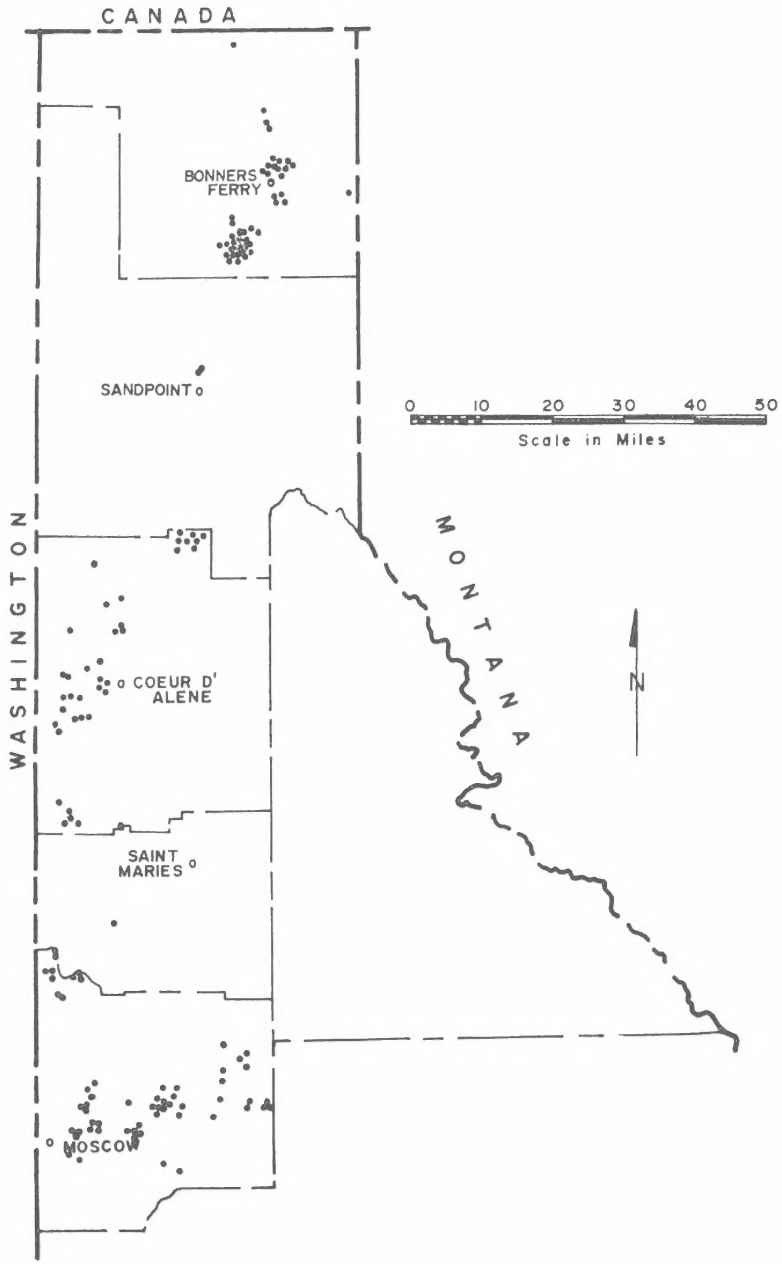

Figure 1. Location map of selected plots in northern Idaho.

of soil-woodland relationships in the area. Since many soil-woodland observations were made in this area, the latter was chosen.

Stepwise multiple regression analyses of the plot data were selected to obtain prediction equations. It was hoped the use of these equations would give a reliable measure of site quality in disturbed areas. Site indexes of the four tree species were used as dependent variables and 10 soil and site factors were used as independent variables. The independent variables, selected from the plot data to represent best soil classification, plot position, and physical soil characteristics, are:

- X_1 elevation in feet
- X_2 latitude in hundreds of degrees
- X_3 soil drainage class
- X_4 depth to C horizon in inches
- X_5 moist soil color of upper 6-inch mineral horizon by Munsell color charts
- X_6 texture of control section (Soil Survey Staff, 1967), field determination
- X_7 moist consistence of the most developed horizon in upper 40 inches, field determination
- X_8 soil subgroup
- X_9 soil family
- X_{10} soil series.

Seven of the 10 independent variables were discrete, so numerical codes had to be adapted for them. Latitude, a continuous variable, was recorded in units of degrees and minutes; therefore, minutes were converted to hundredths of a degree. Soil drainage, an important variable to Mader and Owen (1961), seemed to be a logical choice in this study. Depth to the C horizon was also considered by others (Myers and Van Deusen, 1960) to be an important variable. Moist soil color of the upper 6-inch mineral horizon is locally indicative of vegetative composition. Texture of the control section was selected to reflect the soils' available water-holding capacity. Moist consistence of the most developed horizon in the upper 40 inches was selected to reflect root penetrability. The three lowest categories of the soil classification system were selected as independent variables to establish the relationship between soil classification and site index in northern Idaho.

Results

The regression equations were selected on the basis of insignificant change in coefficients of determination with additional steps of regression. The following prediction equations, coefficients of determination, and standard partial regression coefficients for the four species are:

(ponderosa pine)

$$\hat{Y}=70.95137+1.26319X_9$$

$$R^2=0.45$$

Variable	*Standard partial regression coefficient*
X_9 (family)	0.66930

(lodgepole pine)

$$\hat{Y}= -48.03618+0.03715X_1+6.3169X_7$$

$$R^2=0.41$$

Variable	*Standard partial regression coefficients*
X_1 (elevation)	0.93992
X_7 (moist consistence)	0.75061

(western white pine)

$$\hat{Y} = -1.62242 + 15.28558X_3 + 0.62654X_5$$

$R^2 = 0.64$

Variable	*Standard partial regression coefficients*
X_3 (soil drainage)	0.64289
X_5 (soil color)	0.46585

(western larch)

$$\hat{Y} = 77.26344 + -0.00657X_1 + -0.70319X_8 + 0.59386X_9$$

$R^2 = 0.26$

Variable	*Standard partial regression coefficients*
X_1 (elevation)	–0.41856
X_8 (subgroup)	–0.31534
X_9 (family)	0.55394

Discrete Variable Codes

The following discrete variable codes were used in the prediction equations:

Codes for soil drainage classes (X_3)

excessively drained	1	well drained	3
somewhat excessively drained	2	moderately well drained	4

Codes for moist soil color in upper 6-inch mineral horizon (X_5)

10YR 2/2	01	2.5YR 5/2	19
10YR 2.5/2	02	10YR 4/3	20
10YR 2/2.5	03	10YR 3/3.5	21
10YR 2.5/2.5	04	7.5YR 3/2	22
10YR 4.5/2	05	10YR 3.5/3	23
10YR 3/2	06	10YR 3/4	24
10YR 2.5/3	07	2.5YR 5/1	25
10YR 2/1	08	7.5YR 3/3	26
10YR 3/2.5	09	10YR 3.5/3.5	27
10YR 2/1.5	10	10YR 4/4	28
10YR 4.5/3	11	7.5YR 3.5/2.5	29
10YR 3/3	12	10YR 3.5/4	30
7.5YR 2.5/2	13	7.5YR 3/3.5	31
10YR 4/2	14	7.5YR 4.5/4	32
10YR 3.5/2	15	7.5YR 3/4	33
10YR 5/3	16	7.5YR 3.5/3.5	34
10YR 4/2.5	17	7.5YR 4/4	35
2.5YR 5.5/2	18	7.5YR 3.5/4	36

Codes for moist consistence of the most developed horizon in upper 40 inches (X_7)

loose	1	soft	5
extremely firm	2	friable	6
very firm	3	very friable	7
firm	4		

Codes for soil subgroup (X_8)

Lithic Haploxeroll	01	Boralfic Cryorthod	10
Typic Haploxeroll	02	Typic Fragiochrept	11
Typic Argixeroll	03	Typic Dystrochrept	12
Aeric Argialboll	04	Typic Hapludalf	13
Typic Argiudoll	05	Glossoboric Hapludalf	14
Glossoboralfic Argiudoll	06	Alfic Fragiorthod	15
Dystric Xerochrept	07	Typic Haplorthod	16
Mollic Hapludalf	08	Alfic Haplorthod	17
Typic Cryorthod	09		

Codes for soil family (X_9)

Lithic Haploxeroll loamy-skeletal, mixed, mesic	01
Typic Haploxeroll loamy-skeletal, mixed, mesic	02
Typic Argixeroll loamy-skeletal, mixed, mesic	03
Typic Argixeroll fine-loamy, mixed, mesic	04
Typic Argixeroll fine-silty, mixed, mesic	05
Typic Argixeroll loamy-skeletal, mixed, frigid	06
Typic Haploxeroll coarse-loamy, mixed, frigid	07
Aeric Argialboll fine-montmorillonitic, mesic	08
Glossoboralfic Argiudoll fine-silty, mixed, mesic	09
Dystric Xerochrept sandy, mixed, mesic	10
Typic Argiudoll fine-loamy, mixed, frigid	11
Glossoboric Hapludalf fine, montmorillonitic, mesic	12
Typic Argiudoll fine-silty, mixed, frigid	13
Dystric Xerochrept coarse-loamy, mixed, mesic	14
Mollic Hapludalf loamy-skeletal, mixed, mesic	15
Typic Haplorthod sandy, mixed, frigid	16
Typic Cryorthod loamy-skeletal, mixed	17
Typic Cryorthod coarse-loamy, mixed	18
Boralfic Cryorthod fine-silty, mixed	19
Typic Dystrochrept loamy-skeletal, mixed, frigid	20
Typic Hapludalf loamy-skeletal, mixed, frigid	21
Typic Dystrochrept fine-loamy, mixed, mesic	22
Typic Dystrochrept coarse-loamy, mixed, frigid	23
Typic Fragiochrept fine-silty, mixed, frigid	24
Typic Haplorthod loamy-skeletal, mixed, frigid	25
Typic Haplorthod coarse-loamy over sandy or sandy skeletal, mixed, frigid	26
Typic Haplorthod coarse-silty over sandy or sandy skeletal, mixed, frigid	27
Typic Hapludalf fine-silty, mixed, mesic	28
Mollic Hapludalf fine-loamy, mixed, frigid	29
Alfic Fragiorthod fine-silty, mixed, frigid	30
Typic Hapludalf fine-silty, mixed, frigid	31
Typic Haplorthod sandy over loamy, mixed, frigid	32
Typic Haplorthod coarse-loamy, mixed, frigid	33
Typic Haplorthod coarse-silty, mixed, frigid	34
Typic Haplorthod fine-silty, mixed, frigid	35
Alfic Haplorthod fine-loamy, mixed, frigid	36
Alfic Haplorthod fine-silty, mixed, frigid	37

Discussion

In the prediction equation selected for ponderosa pine, soil family accounted for 45 per cent of the variation in site index. An R^2 value of 0.51 was obtained when all 10 independent variables were introduced.

Elevation and the moist consistence of the most developed horizon in the upper

40 inches accounted for 41 per cent of the variation in site index of lodgepole pine in the prediction equation. Elevation is approximately 25 per cent more important than moist consistence. By using all 10 variables, an R^2 value of 0.62 was obtained.

In the equation selected to predict site index of western white pine, soil drainage and moist soil color of the upper 6-inch mineral horizon accounted for 64 per cent of the variation in site index. Soil drainage is approximately 33 per cent more important than soil color. Seventy-five per cent of the variation in site index is accounted for by using all 10 variables.

Elevation, subgroup, and family accounted for 26 per cent of the variation in site index of western larch in the prediction equation. Soil family is approximately 25 per cent more important than elevation and 75 per cent more important than soil subgroup. Thirty-seven per cent of the variation in site index is accounted for by introducing all 10 variables.

Conclusions

The regression equation for western white pine is a fairly reliable tool for determining site quality for this species in northern Idaho. Soil drainage and moist soil color of the upper 6-inch mineral horizon are the only determinations that need to be made. The equations for ponderosa pine, lodgepole pine, and western larch are less reliable. Use of these equations to determine site quality for these three species should be limited to northern Idaho areas with unknown soil-woodland relationships. More reliable equations for these species could be expected if additional plots were available. Discrete variables (soil color, drainage, etc.) from half of the plots could have been set in linear relationship with the actual site index values and regression equations derived from the other half.

The land manager who elects to use these equations will either require the assistance of a soil scientist to make the necessary observations or must have a good working knowledge of soil classification.

Literature Cited

British Columbia Forest Service. 1947. Lodgepole pine yield tables. 2nd print. Mimeo.

Cummings, L. J. 1937. Larch-Douglas-fir board foot yield tables. U.S. Forest Service, Northern Rocky Mountain Forest and Range Exp. Sta. Applied Note No. 78. 5 pp.

Haig, I. T. 1932. Second-growth yield, stand and volume tables for the western white pine type. U.S. Dept. Agr. Tech. Bull. 323. 67 pp.

Idaho Conservation Needs Committee. 1963. Idaho soil and water conservation needs inventory. U.S. Government Printing Office. 69 pp.

Mader, D. L., and D. F. Owen. 1961. Relationships between soil properties and red pine growth in Massachusetts. Soil Sci. Soc. Amer. Proc. 25(1):62-64.

Meyer, W. H. 1938. Yield of even-aged stands of ponderosa pine. U.S. Dept. Agr. Tech. Bull. No. 630. 60 pp.

Myers, C. A., and J. L. Van Deusen. 1960. Site index of ponderosa pine in the Black Hills from soil and topography. J. Forestry, 58(7):548-555.

Soil Survey Staff. 1951. Soil survey manual. U.S. Dept. Agr. Handbook No. 18. U.S. Government Printing Office, Washington, D.C. (includes supplement dated 1962, p. 173-188). 503 pp.

Soil Survey Staff. 1967. Supplement to soil classification system (7th approximation). U.S. Dept. Agr. Soil Conservation Service. 207 pp.

Wilson, A. K. 1962. Timber resources of Idaho. U.S. Forest Service. Intermountain Forest and Range Exp. Sta. Forest Survey Release No. 3. 42 pp.

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Environmental and Biologic Observations on Contrasting Slopes of Small Earth Mounds*

Introduction

Winter annuals, although not prominent plants of the undisturbed shrub steppe vegetation of southeastern Washington, are important as colonizers of disturbed soil. On disturbed soil cheatgrass, *Bromus tectorum,* an exotic plant, persists for many years. It was expected that the vegetation of contrasting slopes of artificially formed earth mounds would show contrasts in productivity as measured by weekly harvests of above-ground biomass. To our knowledge, there have been no studies made comparing the effect of slope exposure on net production of winter annuals.

This paper presents field observations on the environment and biomass of winter annuals growing on contrasting north and south exposures on small, cone-shaped, artifically formed earth mounds during the spring of 1969. The mounds, each about three meters tall and eight meters in diameter, are located on the Atomic Energy Commission's Hanford Reservation, Benton County, Washington at an elevation of approximately 400 feet above mean sea level (Fig. 1). The mounds were probably made in the early 1950's from *in situ* materials and consist of a heterogeneous mixture of fine-textured glaciofluvial and eolian materials intermixed with quantities of rounded pebbles, gravels, and cobbles. During the existence of the mounds, plant invasion has not been disturbed by man or by grazing domestic animals.

The vegetation growing on the mounds over the past several years has consisted almost entirely of winter annuals, especially cheatgrass (*Bromus tectorum*), tansy mustard (*Descurainea sophia*), tumble mustard (*Sisymbrium altissimum*), and jagged chickweed (*Holosteum umbellatum*). The only perennial plant observed is Sandberg bluegrass (*Poa secunda*) which is mostly restricted to a few scattered clumps on the north-facing slopes. The summer annual, Russian thistle *Salsola kali,* also has grown on the mounds especially the north-facing slopes. However, *Salsola* has not appeared every year.

Methods Employed

Productivity was determined by harvesting above-ground plant parts weekly throughout the most active part of the growing season from mid-March to mid-May 1969. A total of six mounds were used during the study. Every week early in the harvest season, a plot, 1 x 1 foot square, was harvested from the north and south slopes of the

* This paper is based on work performed under United States Atomic Energy Commission Contract AT(45-1)-1830.

Figure 1. Photograph of an earth mound in April. The south-facing slope is on the right. A meter stick is shown for scale.

same three mounds giving a total of six harvested plots per week. Late in the season only the north-facing slopes of another three mounds were harvested yielding three plots per week, *i.e.*, one plot per mound per week.

Plucking plants by hand proved to be the most practical method of plant harvest on the irregular surface. A small portion of the root system was usually attached to each plant as it was pulled and this was included as harvest yield. Plants were collected according to species and placed in paper bags for transport to the laboratory where they were oven dried at 60 C. Biomass is expressed as grams of dry plant material per square foot and also as an average weight per plant.

Continuous records of total incoming solar radiation were made by two clock-driven pyranometers, one on each contrasting slope. The instruments were tilted to approximate the 36° slope angle. Air temperatures were measured near ground level by two thermographs, one on each slope exposure. The instruments were shielded to prevent sunlight from striking the sensing elements directly.

Soil temperatures were made weekly from thermocouples buried four decimeters deep. Soil-moisture determinations were considered but these were impractical to obtain considering the stoniness of the mounds.

Laboratory tests to determine seed germinability were conducted using five lots of 25 seeds each from north and south exposures. Petri dishes were fitted with a disk of filter paper upon which the seeds were placed. The dishes were kept in thermostatically controlled incubators at temperature regimes of 15 and 20 C. After wetting, seeds were kept in the dark except when taken out of the incubators for tallying germinated seeds.

Observations

The 1968-69 growing season throughout the region was marked by an unusually luxuriant growth of winter annuals. The weather during the growth year was characterized by above average monthly precipitation in October and November which promoted the early establishment of seedlings (Table 1). April also brought greater

than average precipitation at a critical stage of growth. Although total precipitation averaged greater than normal the winter temperatures were much colder. January was especially cold with an average temperature of 9.8°F below normal (Table 1).

TABLE 1. Summary of climatic conditions at Pacific Northwest laboratory meterological station during the 1968-69 growing season.

	Avg. temp. °F	Departure from normal	Total monthly ppt.	Departure from normal
1968 Sept.	66.8	+1.0	0.25	−0.09
Oct.	50.3	−3.1	0.93	+0.20
Nov.	41.7	+2.1	1.23	+0.46
Dec.	30.6	−3.3	1.25	+0.38
1969 Jan.	19.8	−9.8	1.24	+0.26
Feb.	31.7	−3.8	0.54	−0.12
March	45.8	+1.4	0.10	−0.38
April	52.2	−1.2	1.22	+0.85
May	64.6	+2.5	0.51	+0.01
Total ppt.			7.27	+1.57

Station Location: Latitude 46° 34′ N, Long. 119° 35′ W, ground elevation 733 feet.

The weekly change in harvest yields from contrasting north- and south-facing slopes throughout the most active parts of the growth season is shown in Table 2.

TABLE 2. Plant biomass grams per square foot, on contrasting slopes of earth mounds during the spring of 1969.

Harvest date	Dry wt. in grams			Mean ± S.E.*	Per cent forbs
	North slope				
3/18	.99	.49	1.06	.85 ± 0.18	0
3/25	2.29	.30	.87	1.15 ± 0.59	21
4/2	1.88	.76	.77	1.13 ± 0.37	25
4/9	2.83	.87	2.70	2.03 ± 0.63	12
4/16	3.27	1.35	1.70	2.10 ± 0.59	24
4/23	3.91	2.63	1.63	2.72 ± 0.69	6
4/30	5.35	1.50	6.84	4.56 ± 1.14	22
5/8	5.47	5.20	6.97	5.88 ± 0.08	20
5/19	13.67	6.10	7.95	9.24 ± 2.28	8
	South slope				
3/18	8.97	5.35	3.97	6.10 ± 1.49	15
3/25	7.04	9.48	1.71	6.08 ± 2.29	12
4/2	15.81	5.62	3.14	8.19 ± 3.88	12
4/9	11.53	16.80	4.62	10.98 ± 3.53	21
4/16	21.46	11.34	8.30	13.70 ± 3.98	19

* S.E.=Standard Error

Cheatgrass provided most of the biomass, tumble mustard contributed between 12 and 21 per cent of the total biomass on the south-facing slopes, while *Holosteum* contributed mostly to the forb biomass on the north-facing slopes.

At the beginning of the spring growing season in mid-March, the average cheatgrass plant on the south exposures weighed much more than those on the north exposures (Table 3). This indicates that the autumn environment was more salubrious on the south exposure. The cheatgrass plants on the south exposures also flowered and matured earlier. By early April at least half of the cheatgrass plants in each harvested plot on the south-facing slope had flowering culms. A similar stage of development was not attained by the north-facing slope plants until early May. By mid-April cheatgrass

TABLE 3. Mean density of cheatgrass plants per square foot and the average weight of individual plants on contrasting slopes of earth mounds during the spring 1969.

Harvest date	Average density/ft^2 ± S.E.	Average wt. per plant (mg)
	North slope	
3/18	80.7 ± 16.9	10
3/25	94.7 ± 34.5	9
4/2	91.7 ± 31.2	8
4/9	129.0 ± 26.8	14
4/16	86.7 ± 14.7	18
4/23	88.3 ± 15.5	31
4/30	144.0 ± 34.1	25
5/8	118.7 ± 18.8	39
5/19	108.7 ± 13.3	78
AVERAGE	104.7 ± 7.8	—
	South slope	
3/18	48.3 ± 8.8	215
3/25	39.7 ± 15.4	133
4/2	51.3 ± 20.1	141
4/9	30.3 ± 3.5	287
4/16	34.0 ± 2.1	387
AVERAGE	40.7 ± 5.1	

plants on the south side had matured and were brown in color indicating that soil moisture was exhausted. However, plants on the north-facing slope continued to grow and remained green throughout April and into May.

When the average total biomass on the contrasting slopes was compared for each harvest day using t tests, the tests were not significant (except for 3/18/69 and 4/16/69) due to the large variability in biomass between plots on a given harvest day. However, a regression analysis described in the next section resulted in statistically significant differences in yields on the two slopes.

Although the growing season was extended several weeks on the north exposures, the terminal average biomass on the south exposure (13.70 gms/ft^2) was about 25 per cent greater than that on the north (9.24 gms/ft^2). However, the difference of 4.46 grams with standard error 4.58 was not statistically significant. A significant result may have been obtained if considerably more than three plots per day per slope had been harvested. We have estimated that approximately 26 plots on each slope would be required to be 80 per cent sure of obtaining a statistical significant result for a true mean difference in yield of 4.5 gm/ft^2.

Total incoming radiation measured on the contrasting slopes showed that south-facing slopes received considerably more solar radiation than north-facing slopes (Table 4). From the first of March until cheatgrass maturation in mid-April the

TABLE 4. Weekly accumulative solar radiation (langleys) on contrasting slopes of a small earth mound measured during the spring of 1969.

Date	North	South
3/18	1,100	2,800
3/25	2,200	7,700
4/2	4,200	*12,000
4/9	6,300	15,900
4/16	8,400	19,900
4/23	10,800	
4/30	*13,300	
5/8	16,900	
5/19	22,400	

* Flowering of cheatgrass.

south-facing slope received 19,900 langleys. At the same time the north-facing slope had received only 8,400 langleys. However, the north-facing slope had accumulated a total input of approximately 22,000 langleys at cheatgrass maturity in May.

The higher input of solar energy to the south exposure resulted in higher soil temperatures, and daytime air temperatures (Fig. 2). Nighttime air temperatures on the south slope also averaged slightly higher, but the contrasts were not so apparent as were the daytime temperatures.

The large variations observed in the harvested biomass between plots on a given day appeared to be due to two factors. First, the slope surfaces had exposed stones, some quite large, which determined the amount of surface available for plant rooting. There also was a great deal of observed variation in the sizes of individual plants. This became increasingly apparent as the growing season progressed. Some cheatgrass plants at maturity had culms 3-4 dm tall with numerous basal leaves and several flowering culms, each with dozens of florets. Other plants were very small, 3-4 cm tall, with only a pair of basal leaves and a single flowering culm with only a few florets. The large differences in plant sizes are presumably due in part to the volume of soil and concomitant moisture-storage volume available to the roots of each plant as determined by the arrangement and amount of rock and the amount of competition from neighboring plants.

The north slopes averaged more plants per square foot than did the south slopes (Table 3). In studies concerning competition among weedy species, Palmblad (1968) showed that the seeds of greenhouse-grown cheatgrass under high stand density conditions averaged less in weight as compared to seeds produced under low density. It was expected that the more dense stands of cheatgrass would produce small plants with smaller seeds.

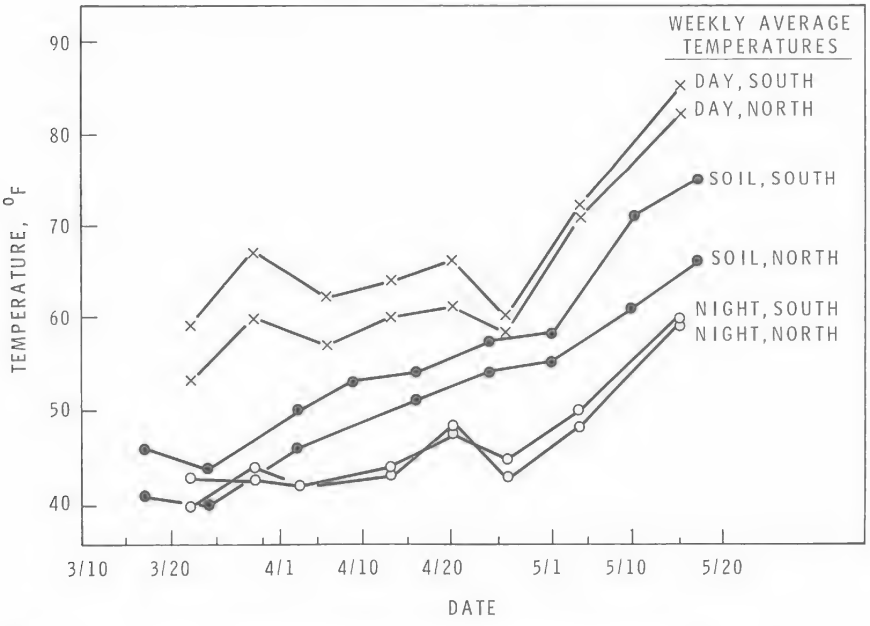

Figure 2. Weekly average air and soil temperatures on north- and south-facing slopes.

However, the average weights of five lots of 25 seeds each from the north and south slope were 0.0586 and 0.0600, respectively. This difference in average weight of 0.0014 grams with pooled standard error of .000842 was not statistically significant at the .05 level.

Palmblad (1968) reported germination percentages ranging between 84-87 per cent for laboratory-grown cheatgrass seeds produced under different stand densities. Germinability of cheatgrass seeds from the earth mound was also high but the south slope seeds did not germinate so promptly as did the north slope seeds, especially under the cooler temperature regime (Fig. 3). Similar results have been reported previously (Rickard and Hinds, 1969). The significance of delayed germination is not clear but it may be important to the successful establishment of seedlings on the more xeric south slopes. Seeds that do not readily germinate early in autumn would appear to have a better chance to avoid drought than prompt germinators because of the greater likelihood of increased frequency and intensity of precipitation associated with the approach of winter.

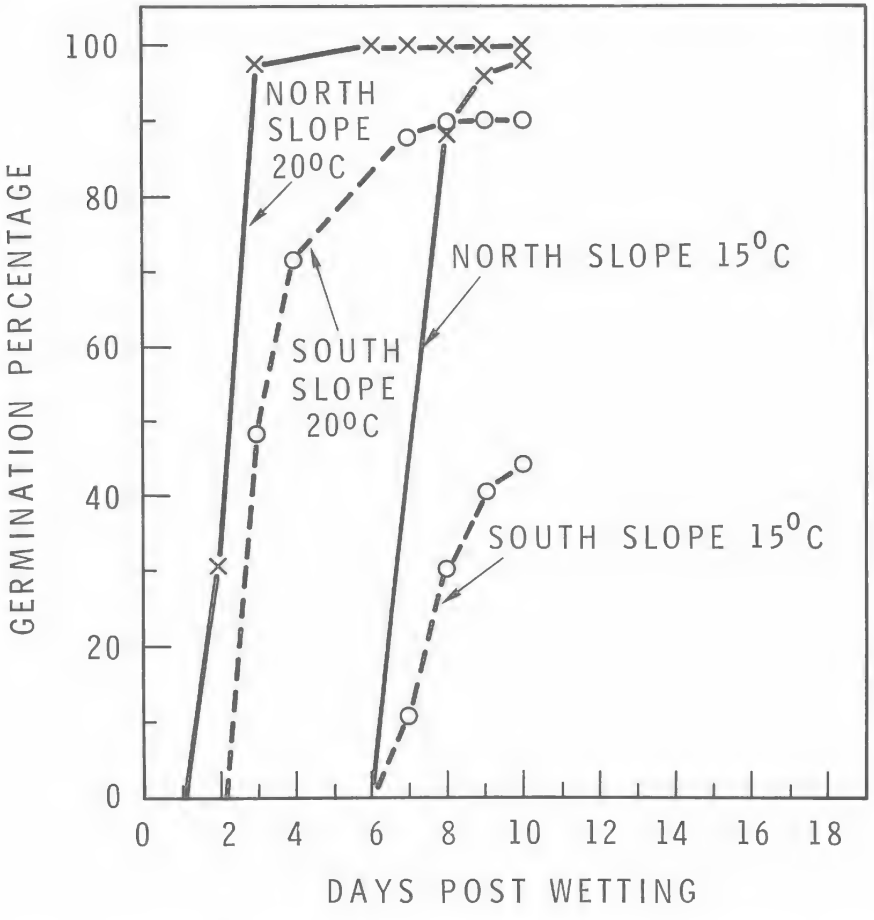

Figure 3. Germination percentage of cheatgrass seeds collected from north- and south-facing slopes under 15 and 20 C temperature regimes.

One way to employ effectively the different microclimates of contrasting slope exposures for biologic and environmental observations, without the high degree of variability associated with a heterogeneous substrate, is to construct purposefully mounds of rock-free soil. Such mounds would permit meaningful measurements of soil moisture, which is of special significance to winter annuals since growth terminates with the spring depletion of soil moisture.

Biomass—Time Models

A plot of the average biomass G_i harvested on day i against the cumulative number of days since the first harvest day X_i, suggests that the J-shaped exponential growth model

$$G_i = Ae^{cX_i} \tag{1}$$

may fit both the north and south slope data over the time period for which harvests were made ($i = 1, \ldots, 5$ – south data: $i = 1, \ldots, 9$ – north data), where A is the biomass on the first day, and c is the overall population growth rate under unlimited environmental conditions (Odum, 1959, p. 178). In our study

$$G_i = \frac{1}{3} \sum_{j=1}^{3} G_{ij}$$

where G_{ij} is the biomass harvested from the jth plot on day i. Rather than estimate A and c under the exponential model above, which would require the solution of nonlinear equations in A and c by successive approximations, we have taken the simpler route of transforming equation (1) by taking $\log_e$ of both sides. Our model is thus

$$Y_i = \log_e G_i = \log_e A + cX_i + \varepsilon_i \tag{2}$$

or

$$Y_i = \alpha + cX_i + \varepsilon_i \tag{3}$$

where $\alpha = \log_e A$ and the residuals ε_i are assumed to be normally and independently distributed with a mean of zero and variance σ^2.

Under the linear form given in equation 3 the least squares estimates $\hat{\alpha}$, $\hat{c}$, and $\hat{\sigma}^2$ as well as tests of significance and confidence limits on c are readily available. These estimates and the resulting fitted models in both the linear and exponential forms are given in Tables 5, 6, and 7 and Figures 4 and 5. Tests of significance in Table 7 in-

TABLE 5. Observed and expected biomass under the model $\log \hat{G}_i = \hat{\alpha} + \hat{c}\, X_i$.

X	North slope		South slope	
	Observed	Expected	Observed	Expected
0	–.1625	–.252	1.8077	1.7033
7	.1398	.273	1.8045	1.9133
15	.1222	.333	2.1029	2.1533
22	.7080	.606	2.3961	2.3633
29	.7419	.879	2.6174	2.5733
36	1.0006	1.152	—	—
43	1.5173	1.425	—	—
51	1.7716	1.737	—	—
62	2.2235	2.166	—	—

TABLE 6. Observed and expected biomass under the model $\hat{G}_i = \hat{A}e^{\hat{c}X_i}$

X	North slope Observed	North slope Expected	South slope Observed	South slope Expected
0	.85	.777	6.10	5.492
7	1.15	1.021	6.08	6.775
15	1.13	1.395	8.19	8.613
22	2.03	1.833	10.98	10.626
29	2.10	2.408	13.70	13.109
36	2.72	3.164	—	—
43	4.56	4.157	—	—
51	5.88	5.678	—	—
62	9.24	8.721	—	—

TABLE 7. Estimated parameters for the linear and exponential models of the relationship between time and total biomass.

	North slope	South slope
$\hat{c}$	0.039	0.030
$\hat{\alpha}$	−0.252	1.704
$\hat{\sigma}^2$	0.0188	0.00938
$\hat{\sigma}_e$	0.00236	0.00420
t test on c	$t=16.54$ (d.f.=7)*	$t=7.223$ (d.f.=3)*
95% conf. limits on c	.033, .045	.017, .044
Linear model	$\log_e \hat{G}_i = -.252 + .039 X_i$	$\log_e \hat{G}_i = 1.704 + .03 X_i$
$e^{\hat{\alpha}} = \hat{A}$	0.777	5.493
Expon. model	$\hat{G}_i = .777\ e^{.039 X_i}$	$\hat{G}_i = 5.493\ e^{.03 X_i}$

* Statistically significant at $\alpha = .05$ level

dicate the $c > 0$ for both north and south slopes. $\hat{A}$ was obtained from $\hat{\alpha}$ as $\hat{A} = e^{\hat{\alpha}}$. These parameters were estimated assuming the linear model given in equation 3; hence, strictly speaking, they are not the least squares estimators under the exponential model. The data are seen to fit quite well both the linear and exponential forms.

TABLE 8. Comparison of the estimated linear regression lines for total biomass on north and south slopes.

	d.f.	Σx^2	Σxy*	Σy^2	$\hat{c}$	Deviations from regression d.f.	S.S.	M.S.
Within								
North	8	3386.222	131.9839	5.2760	.039	7	.131702	.0188
South	4	533.2	16.1562	0.5177	.030	3	.028147	.00938
						10	.159249	.01598
Pooled	12	3919.422	148.1401	5.7937	.0378	11	.194525	.01768
		Difference between slopes				1	.034676	.034676
Between	1	708.292	−59.6380	5.0215				
Pooled + Between	13	4627.714	88.5021	10.8152		12	9.12265	
		Between adjusted means				1	8.92813	8.92813

Comparison of residual variances: $F = .0188/.00938 = 2.00$ (d.f.=7, 3) N.S.
Comparison of slopes: $F = .034676/.0159849 = 2.169$ (d.f.=1, 10) N.S.
Comparison of elevations: $F = 8.92813/.017684 = 504.87$ (d.f.=1, 11), highly significant.
* $x = X_i - \bar{X}$, $y = Y_i - \bar{Y}$

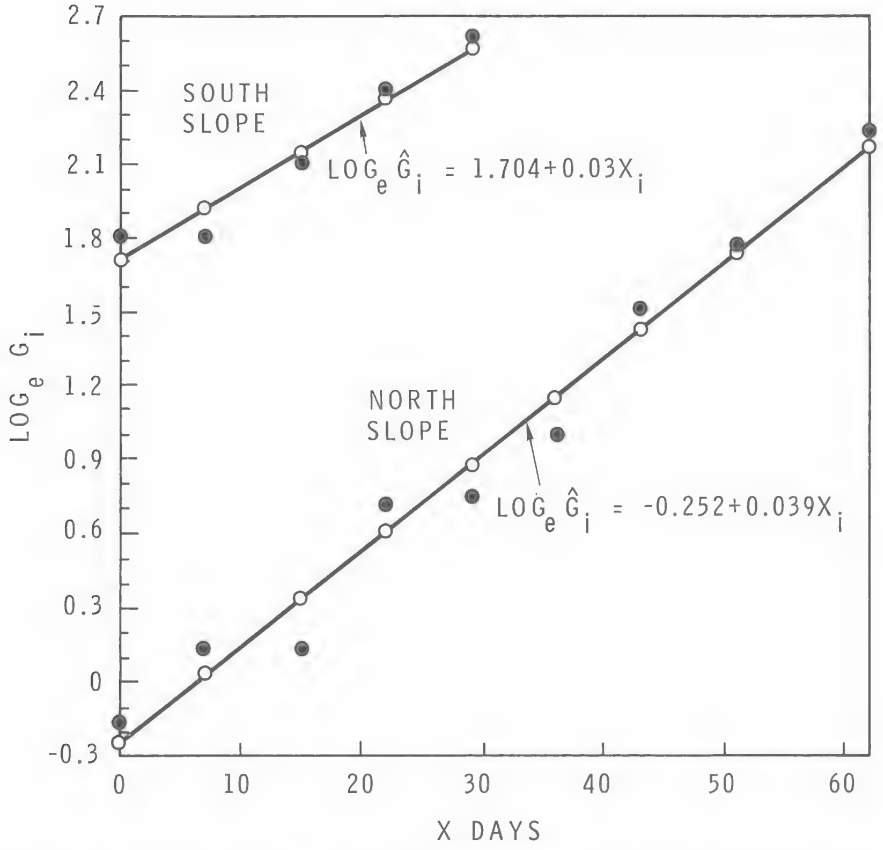

Figure 4. Fitting transformed north- and south-facing slope biomass means $\log_e G_i$ to the straight line $\log_e \hat{G}_i = \hat{\alpha} + \hat{c}\, X_i$

In Table 8 we follow the format given in Snedecor and Cochran (1967, p. 435) for comparing the north and south exposure linear regression lines with respect to residual variation σ^2, slope c, and elevation α above the abcissa. The test results indicate that neither the residual variance nor the slopes of the two regression curves are significantly different. However, the F test of the difference in elevations of the two curves is statistically significant. These results point to the conclusion that in the transformed scale log G_i, the relative rate of increase in biomass per unit of time is approximately the same for the north and south slopes during the spring growing season, but that the amount of biomass measured on a given day during the harvest period studied is substantially greater on the south slope. We recall that this could not be established for most given harvest days by using individual t tests because of the large variability between plot to plot biomass.

An attempt was also made to fit the linear model to the three individual biomass samples per day over the harvest period (Table 2). However, due to the large variability between plots on a given day, the fit was much less satisfactory. For the north slope c was estimated to be .039 with variance $\sigma_c^2 = .0000251$, and 95 per cent confidence limits of (.029, .049). For the south side $\hat{c}$ was .031 with variance $\sigma_c^2 =$

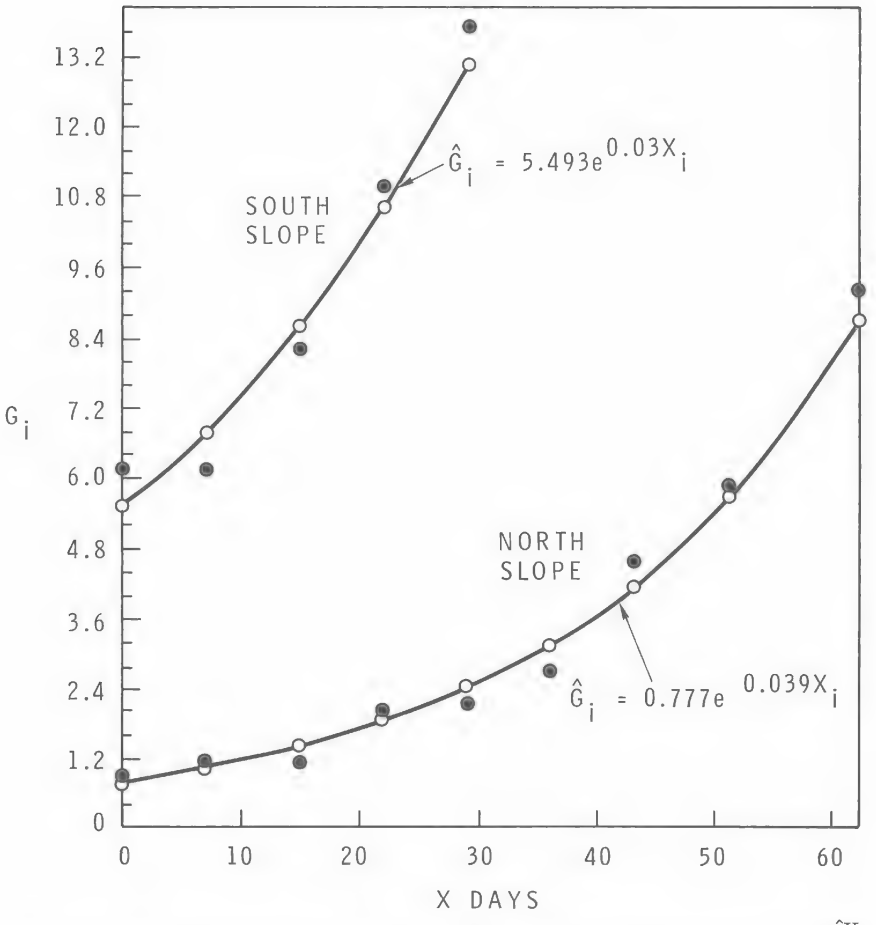

Figure 5. Fitting the north- and south-facing slope biomass means G_i with the curve $\hat{G}_i = \hat{A}e^{\hat{c}X_i}$.

.000241 so that the t test of H_o: c = o was nonsignificant, *i.e.,* the variability was so great on the south side that even though the data show the biomass to be increasing, the statistical test showed no significance. Clearly, when considering individual harvest plots rather than the mean of plots on a given day, many samples are required to obtain a relatively precise estimate of c.

Field Considerations

Phenological criteria have been frequently used in field studies to relate the responses of natural plant communities and the environments of steep slopes and contrasting exposures. In a study of eastern North American deciduous forest herbs, Jackson (1966) reported a maximum variation at time of flowering of 11 days for *Phacelia bipinnatifida* growing on contrasting north and south slopes. In our study cheatgrass was delayed 3 weeks in flowering on the north slope. This lag is indicative of the strong influence that the abiotic environment has upon the phenological response of

plants in a shrub steppe region. Biotic factors also play an important role in determining the floristic composition of plant communities. Since the introduction of Eurasian weeds to Western North America about 100 years ago, cheatgrass has become an integral part of the flora of disturbed habitats, thereby changing the species composition and general appearance of the shrub steppe communities of southeastern Washington. Under undisturbed conditions the native Sandberg bluegrass occurs on all slope angles and exposures. The apparent inability of Sandberg bluegrass to colonize the south-facing slopes of the earth mounds after approximately 15 years suggests that a combination of factors, *i.e.,* cheatgrass competition and a warmer and drier microclimate on steep south-facing slopes are deterrents to bluegrass establishment. Other evidence that cheatgrass and south-facing slopes are effective deterrents to perennial grass establishment is provided by Dillon (1967). After 64 years of nongrazing use, the south exposure of an earthfill supporting a railroad track in southeastern Washington was vegetatively dominated by winter annuals, especially cheatgrass. The north-facing slope, however, supported the typical dominants of climax communities, especially bluebunch wheatgrass *Agropyron spicatum* and *Poa secunda.* Harris (1967) showed laboratory and field experiments that seedlings of cheatgrass are more competitive than those of bluebunch wheatgrass.

Artificial earth mounds purposefully constructed of rock-free soil would appear as a way to minimize substrate variability and to produce a variety of field environments for study at relatively low cost. The opportunity to alter outdoor environments by the expeditious designing of slope angles and exposures would seem to be useful in the system-oriented research advocated by the International Biological Program projects in the desert and grassland biomes.

Summary

A series of simple biologic and environmental observations were made on small cone-shaped earth mounds in the shrub steppe region of Washington in the Spring of 1969. The environment on contrasting north- and south-facing slopes was marked by high solar radiation inputs on the south-facing slopes which resulted in higher soil and air temperatures throughout the spring growth period of winter annuals. There was a marked difference in time of onset of flowering in cheatgrass, *Bromus tectorum,* on the contrasting slopes. Flowering was delayed about three weeks on the north-facing slope. North slope stands were more dense than south slope stands. Seeds from the south slope did not germinate so quickly under laboratory conditions as north slope seeds. This was especially marked under a colder temperature regime.

The mean biomass of plant material produced on the south-facing slope substantially exceeded that of the north-facing slope on a given harvest day. This difference in yield was statistically significant when the linear relationship between average biomass harvested and time since first harvest day was taken into account. The north and south linear regression lines appear to have the same slope, which implies that both north and south exposures may have the same relative rate of growth, at least over the period of time observed in this study.

Literature Cited

Dillon, C. C. 1967. Exposure may influence grassland establishment. J. Range Mgt., 20(2): 117-118.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum.* Ecol. Monogr., 37(2): 89-111.

Jackson, M. T. 1966. Effects of microclimate on spring flowering phenology. Ecology, 47: 407-415.
Odum, E. P. 1959. Fundamentals of Ecology, 2nd ed. Saunders Co., Philadelphia, p. 546.
Palmblad, L. B. 1968. Competition in experimental populations of weeds with emphasis on the regulation of population size. Ecology, 49(1): 26-34.
Rickard, W. H., and W. T. Hinds. 1969. Observations on the growth of cheatgrass on a small earth mound. Pacific Northwest Laboratory Report for 1968. AEC Res. and Devel. Report. BNW 1050 Part 2. pp. 1.29-1.33.
Snedecor, G. W., and W. G. Cochran. 1967. Statistical Methods, 6th Edition, Iowa State University Press, Ames, Iowa, pp. 593.

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Food Habits of the Burrowing Owl in Central Oregon

Little appears to be known about the food habits of burrowing owls (*Speotyto cunicularia*) in central Oregon. Bent (1938) includes general statements by a number of individuals about the prey of the burrowing owl from various localities. For example, on page 390, Bent states that in Washington C. E. McBee found "25 mice and 3 sage rats" in one burrow and "15 mice and 2 sage rats" in another. What McBee meant by "sage rats" is not clear. The ranchers within the vicinity of our study area called both the Belding ground squirrel (*Spermophilus beldingi*) and the Townsend ground squirrel (*Spermophilus townsendi*) "sage rats." Some ranchers further distinguished *S. townsendi* to be the young of *S. beldingi.* In addition, Jewett found "four kangaroo rats, two pocket mice, two lizards, and one horned toad, all freshly killed" in a burrowing owl's nest "near Boardman" in April 1932 (Gabrielson and Jewett, 1940).

During a year's study of the sage vole (*Lagurus curtatus*) in the Crooked River National Grassland, Jefferson Co., Oregon, Hammer and Maser (in preparation) discovered that the burrowing owl was the main predator of the sage vole. Throughout the entire year, only three pairs of owls were found—young were not seen. Therefore, as much data as possible were collected and analyzed.

Pellet contents were analyzed in the following manner: (1) computation of prey species composition for the summer, fall, winter, spring, and entire year, and (2) computation of prey species diversity for the summer, fall, winter, spring, and entire year.

Methods

Most pellets were collected from the owls' nesting burrows which were old badger (*Taxidea taxus*) burrows. Some were gathered on and around an old cow chip; others were picked up from an active ant hill. The pellets were easily identified by their size, shape, and location. Furthermore, the owls were almost always seen.

Three hundred forty-seven pellets were analyzed comprising 1,151 prey individuals. All of the pellets were fresh monthly. The burrowing owl pellets were not held together by as much mucus, nor were they invaded and broken down by moth larvae (Tineidae) as were the pellets of other owl species with which we have worked. They had only a slight mucus coating and were only inappreciably slimy when soaked in water during dissection. However, in the field, especially during the winter, the pellets break down readily.

Pellets were collected into plastic bags, soaked in water, and dissected. The prey remains were identified and the individuals counted. Identification of the microtines was based upon Maser and Storm (1970). The other prey species were identified with the aid of the Puget Sound Museum of Natural History collection (Maser and Brodie, 1966). However, in the present study the total number of prey individuals is utilized rather than the number of prey individuals per pellet. The collection is in the Puget Sound Museum of Natural History.

For the purpose of this study, the following months constitute the four seasons: (1) summer—July, (2) fall—October, (3) winter—February, March, April, and (4) spring—May. The number of pellets examined per season is: (1) summer—60, (2) fall—20, (3) winter—228, and (4) spring—39. We realize that the extreme variation in pellet number per season will bias the data to some extent; however, Loren K. Russell (personal comm.) indicated that the seasonal activity of the insects corresponded well with the relative numbers of individuals of the various species found in the owl pellets at a given season. Furthermore, the distribution of mammalian species is about what we have learned to expect.

Due to the growth of vegetation and movement of grazing cattle, whole pellets were difficult to find during the spring, summer, and fall. Further, the pellets were scattered throughout the rabbitbrush and sagebrush, making them extremely hard to find. The cattle were taken out of the study area during the winter—hence the pellets were not smashed. Also, there seemed to be a greater tendency for the owls to cast their pellets in the vicinity of the mouths of their burrows during the winter.

To compare the prey during the different seasons, prey species diversity calculations were made using the formula $H = -\sum_{i=1}^{s} p_i \log_e p_i$ where s is the number of species, p_i is the proportion of the total number of individuals which belong to the ith species (Shannon and Weaver, 1949). Essentially, species diversity is a predictive value answering the question, with what efficiency can the species of the next individual sampled be predicted?

Location and Habitat

All pellets were collected in the Crooked River National Grassland, Jefferson Co., Oregon, in 1969 (Table 1).

The habitat was similar in all areas—open, rolling country. Major vegetation was wheatgrass (*Agropyron* sp.), green rabbitbrush (*Chrysothamnus viscidiflorus*), gray rabbitbrush (*Chrysothamnus nauseosus*), sagebrush (*Artemisia* sp.), and occasional junipers (*Juniperus occidentalis*).

TABLE 1. Locations of pellet collections.

Location	Month
T.12S;R.13E;Sec.13.	February
T.12S;R.13E;Sec.24.	May
T.12S;R.13E;Sec.24.	October
T.12S;R.14E;Sec.13.	March
T.12S;R.14E;Sec.17.	March
T.12S;R.14E;Sec.19.	July
T.13S;R.14E;Sec.6.	April
T.13S;R.14E;Sec.6.	July
T.13S;R.14E;Sec.7.	April

TABLE 2. Prey species of the burrowing owl according to total individual count for the year.

Prey	Summer	Fall	Winter	Spring	Total
Lagurus curtatus	48	12	218	17	295
Nicrophorus hecate	43	3	98	23	167
Perognathus parvus	20	7	89	23	139
Peromyscus maniculatus	5	1	59	2	67
Stenopelmatus sp.	16	..	34	9	59
Formica sp.	35*	....	1	1	37
Paracotalpa granicollis	1	1	....	32	34
Coleoptera	2	1	25	2	30
Cricetidae	6	2	13	8	29
Coniontis sp.	6	2	11	7	26
Thomomys talpoides	2	3	18	....	23
Eleodes sp.	....	...	17	3	20
Ctenicera sp.	16	....	....	1	17
Calosoma luxatum	10	....	2	1	13
Trox atrox	5	....	6	2	13
Diplotaxis sp.	....	3	7	2	12
Nicrophorus sp.	7	....	4	1	12
Scarabaeidae	1	8	3	.. .	12
Orthoptera	....	....	9	2	11
Carabidae	2	....	6	1	9
Formicidae	2	1	6	....	9
Microtus montanus	....	1	8	.. .	9
Amara sp.	....	. ...	2	6	8
Polyphylla decemlineata	5	...	3	....	8
Tenebrionidae	1	2	5	....	8
Cymindis sp.	3	....	1	3	7
Anisodactylus sp.	1	....	4	1	6
Aves	2	....	3	1	6
Lagomorpha	1	....	5	....	6
Phobetus comatus	...	...	3	3	6
Cicadidae	2	....	3	. ..	5
Dipodomys ordi	2	1	2	....	5
Hymenoptera	..	....	3	2	5
Insecta	....	4	1	....	5
Curculionidae	3	..	1	....	4
Reithrodontomys megalotis	1	....	2	.. .	3
Aphodius sp.	1	....	....	1	2
Cicindela longilabris	2	....	....	....	2
Dermaptera	..	. ..	. ..	2	2
Dyslobus sp.	1	....	1	....	2
Elateridae	1	...	1	....	2
Nicrophorus nigritus	....	....	2	....	2
Nicrophorus marginatus	1	1	....	....	2
Boreocanthon simplex	2	....	....	....	2
Scorpionida	....	....	2	....	2
Acrididae	....	....	....	1	1
Camponotus sp.	....	....	....	1	1
Euphoria sp.	...	....	1	....	1
Glyptoscelis sp.	....	. ..	....	1	1
Lepidoptera larva	1	....	. ..	...	1
Lophortyx californicus	1	....	....	....	1
Microtinae	....	1	....	....	1
Sceloporus sp.	1	....	. ..	....	1
Total species	37	17	40	29	54
Total individuals	258	53	679	159	1151

*All 35 *Formica* sp. were in one pellet.

Results and Discussion

Due to the great diversity, prey species will be discussed collectively by Class and Order, except Coleoptera which will be discussed by Family.

TABLE 3. Prey species by Class, Order, and number of individuals.

Prey	Summer	Fall	Winter	Spring	Total
Class					
Mammalia	85	28	414	50	577
Order					
Rodentia	84	28	409	50	571
Lagomorpha	1	----	5	----	6
Class					
Insecta	170	22	259	108	559
Order					
Coleoptera	114	21	203	90	428
Orthoptera	16	----	43	12	71
Hymenoptera	37	1	10	4	52
Homoptera	2	----	3	----	5
Dermaptera	----	----	----	2	2
Lepidoptera	1	----	----	----	1
Class					
Aves	3	----	3	1	7
Order					
Passeriformes	2	----	3	1	6
Galliformes	1	----	----	----	1
Class					
Arachnida	----	----	2	----	2
Order					
Scorpionida	----	----	2	----	2
Class					
Reptilia	1	----	----	----	1
Order					
Squamata	1	----	----	----	1

Mammalia

Rodentia

The sage vole (*Lagurus curtatus*) was by far the most important prey species on a yearly basis, especially during the fall and winter. These voles were readily available because the owls' nesting burrows were in the midst of *Lagurus* habitat with a good vole population. Sage voles operate on a 24-hour schedule, and we have found fresh owl kills during the day. The owls drop or swoop upon the voles from the tops of sagebrush and rabbitbrush, this being the most common hunting method in our study. They also wait next to the voles' runways and catch them as they run by. We have also found burrowing owl pellets next to *Lagurus* runways and burrows.

The Great Basin pocket mouse (*Perognathus parvus*) sustained the heaviest predation during the winter. These mice are not only common but also forage in open areas and are relatively slow, making capture easy. The deer mouse (*Peromyscus maniculatus*), on the other hand, move quickly and stay close to cover. The heavy winter toll is probably due to seasonal dying of the vegetative cover which, during lack of snow cover, exposes the ground and the small mammals; there were frequently long periods without appreciable snow cover. During the spring, summer, and fall, under the protection of vegetation, these mice would not be easily caught.

The northern pocket gopher (*Thomomys talpoides*) was preyed upon mostly during the winter. These gophers are active throughout the night as well as in the early morning and early evening. They would be most easily captured by an owl hunting on the ground by the burrow entrance, since the gophers are not very active above ground when it is frozen, but without the cover of snow.

The montane vole (*Microtus montanus*) was not particularly numerous within the study area, probably due to lack of adequate grass cover and water. However, we found voles to frequent runways of the sage vole during the winter, but not during the other seasons. This brought them into the hunting range of the burrowing owls.

The Ord kangaroo rat (*Dipodomys ordi*) was not as common in the grassland as in adjacent areas. It, like the pocket mouse, forages in the open; therefore, both mammals would be vulnerable prey to a burrowing owl perched quietly on top of a bush. However, the kangaroo rat was not an important food item.

Harvest mice (*Reithrodontomys megalotis*) were relatively common, but their small size, quick movements, and affinity to cover would not make them an easy target.

Lagomorpha

Both the mountain cottontail (*Sylvilagus nuttallii*) and the black-tailed jackrabbit (*Lepus californicus*) were found within the study area. Cottontails were not very numerous during 1969. Since the lagomorph remains were fragmented, it was not possible to identify them with certainty to species. However, those caught during the winter were thought to be cottontails because jackrabbits would probably have been too large.

Insecta

Coleoptera

TABLE 4. The families of Coleoptera and seasonal distribution in pellets.

Family	Summer	Fall	Winter	Spring	Total
Silphidae	51	4	104	24	183
Scarabaeidae	15	12	23	40	90
Tenebrionidae	7	4	33	10	54
Carabidae	16	----	15	12	43
Elateridae	17	----	1	1	19
Curculionidae	4	----	2	----	6
Cicindelidae	2	----	----	----	2
Chrysomelidae	----	----	----	1	1
Total	112	20	178	88	398

Silphidae. The burying beetles were represented by three species: (1) *Nicrophorus hecate,* (2) *Nicrophorus marginatus,* and (3) *Nicrophorus nigritus. N. hecate* was the second-most important prey species to the burrowing owl during the winter and summer, respectively. While beetles of the genus *Nicrophorus* are largely night fliers, with highest activity just after dark, and could be taken on the wing, the owls were observed catching them during the day around carcasses of winter-killed large mammals. Such carcasses harbored many burying beetles during the winter, especially late winter. Droppings indicated that the owls perched on the top and edge of the carcasses. The owls were observed on the ground around the carcasses and may have dug some of the beetles out from under them, which might explain the high number of pellets (56) containing pebbles (95) during the winter. Pebbles ranged from 1 x 1 mm. to 12 x 9

mm. The number of pebbles/pellet varied from 1 to 9. In addition, 34 pellets contained vegetation (stems and roots) along with quantities of soil.

During the summer, fall, and spring there were numerous dermestid beetles (Dermestidae: *Dermestes marmoratus*) under the carcasses. These beetles were more numerous and were exposed much more often than *Nicrophorus,* but none were taken by the owls.

Scarabaeidae. The following scarab beetles were identified from the pellets: (1) *Paracotalpa granicollis,* (2) *Diplotaxis* sp. (these beetles were so fragmented that they could seldom be determined to species, but *D. brevicollis* and *D. subangulata* were present), (3) *Trox atrox,* (4) *Polyphylla decemlineata,* (5) *Phobetus comatus,* (6) *Aphodius* sp., (7) *Boreocanthon simplex,* and (8) *Euphoria* sp. Most of these scarabs are crepuscular and/or nocturnal; however, *Paracotalpa granicollis, Boreocanthon simplex,* and *Euphoria* sp. are diurnal fliers.

During the spring, *Paracotalpa granicollis* was the most important prey species; only two were taken the rest of the year. None of the other scarabs were taken in large numbers in any season.

Tenebrionidae. Only two genera of darkling beetles were identifiable: *Coniontis* sp. and *Eleodes* sp. Both were common within the study area. These genera are nonflying, ground dwellers and sustained the heaviest predation during the winter. Also taken in the winter were five of the unidentifiable tenebrionids.

Carabidae. The following ground beetles were determined: (1) *Calosoma luxatum,* (2) *Amara* sp., (3) *Cymindis* sp., and (4) *Anisodactylus* sp. The diurnal *Calosoma luxatum* represented 10 of the 16 ground beetles captured in the summer. No carabids were eaten in the fall, but 15 were caught during the winter. Six out of 11 carabids preyed upon in the spring were *Amara* sp. Forty-three carabids were caught throughout the year, making them, with respect to the Coleoptera, relatively important in the owls' diet.

Elateridae. Only the genus, *Ctenicera* sp., of click-beetle could be determined. Seventeen of the 19 elaterids were *Ctenicera* sp., and of the 17, 16 were captured during the summer.

Curculionidae. Six weevils were found in the pellets; two were determined to be *Dyslobus* sp.; four of the six weevils were captured during the summer.

Cicindelidae. Two *Cicindela longilabris* were taken in the summer. These tiger beetles were active during the heat of the day, from approximately 1100-1500 hours.

Chrysomelidae. One *Glyptoscelis* sp. was the only leaf beetle found. The genus is diurnal.

Orthoptera

Seventy-one orthopterans were found in the pellets, 59 Jerusalem crickets (*Stemopelmatus* sp.), one grasshopper (Acrididae), and 11 undetermined. *Stemopelmatus,* a ground dweller, ranked fifth during the winter and spring and shared fifth place with *Ctenicera* (Elateridae) in the summer. None were taken in the fall. Further, *Stenopelmatus* ranked fifth on a yearly basis. Nine of the undetermined orthopterans were captured during the winter; the grasshopper in the spring.

Hymenoptera

Fifty-two hymenopterans were caught throughout the year, 47 were ants, including 37 *Formica* sp. and one *Camponotus* sp. Thirty-five *Formica* were eaten during the summer;

the *Camponotus* was taken in the spring. *Formica* ranked third for total prey in the summer; however, these ants are so small that, nutritionally, they would be of little consequence. Furthermore, 35 of the 37 *Formica* were gleaned from a single pellet.

Aves

In addition to the six passerine birds and the one California quail listed in Table 1, three of the owl pellets contained the crushed shells of birds' eggs, one in March and two in April. Gabrielson and Jewett (1940) report that in Oregon burrowing owls have been found to lay eggs as early as April. The egg shell fragments may indicate that the owls had an early brood. Although we cannot find a reference in the literature to the habit of burrowing owls eating the discarded egg shells of their newly hatched young, it seems to be a possibility.

Arachnida

Scorpionida

While scorpions were common in some parts of the study area they were not particularly abundant around the owls' burrows.

Reptilia

Squamata

One lizard (*Sceloporus* sp.) was taken by the owls. It was either a fence lizard (*S. occidentalis*) or a sagebrush lizard (*S. graciosus*). Both occurred within the study area.

Conclusions

Owls

Major Charles E. Bendire is quoted in Bent (1938, p. 389) as follows:

> They [burrowing owls] hunt their prey mostly in the early evening and throughout the night, more rarely during the daytime. As soon as the sun goes down they become exceedingly active, and especially so during the breeding season. At such times they are always busy hunting food, and go and come constantly, and they may often be seen hovering suspended in the air like the Sparrow Hawk, locating their prey or darting down noiselessly and swiftly, and grasping it with their talons without arresting their flight an instant.

Our experience, over a year's time and approximately 200 days of observation, differed from the above in several respects: (1) the owls were observed hunting during all hours of the days; (2) much hunting was done on the ground as evidenced by observation, by tracking the owls, and by the many pebbles and plant roots in their pellets; and (3) the owls often hunted from rabbitbrush and sagebrush tops from which they would "drop" or "swoop" upon their prey. We did not observe the owls ". . . hovering suspended in the air like a Sparrow Hawk. . . ."

Prey

Prey species diversity was highest in the summer and spring, in that order. During the fall and winter, the prey species diversity was low because of concentration on the sage vole (*Lagurus curtatus*), the burying beetle (Silphidae: *Nicrophorus hecate*), and the Great Basin pocket mouse (*Perognathus parvus*). See Table 5.

TABLE 5. Prey species diversity. . $H = -\sum_{i=1}^{5} p_i \log_e p_i$ (Shannon and Weaver, 1949).

Summer	Fall	Winter	Spring	Total for year
2.760	2.467	2.547	2.656	2.822

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Literature Cited

Bent, A. C. 1938. Life histories of North American birds of prey, part two. Smithsonian Institution United States National Museum Bull. 170. 482 pp.

Gabrielson, I. N., and S. G. Jewett. 1940. Birds of Oregon. Oregon State College, Corvallis, Oregon. 650 pp.

Maser, C., and E. D. Brodie, Jr. 1966. A study of owl pellet contents from Linn, Benton, and Polk Counties, Oregon. Murrelet, 47(1):9-14.

Maser, C., and R. M. Storm. 1970. A key to microtinae of the Pacific Northwest (Oregon, Washington, Idaho). O.S.U. Book Stores, Inc., Corvallis, Oregon. 162 pp.

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. Univ. of Ill. Press, Urbana. 117 pp.

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Biosystematics of the Genus Tiarella in the Washington Cascades

The genus *Tiarella* is a member of the Saxifragaceae family in which it is distinguished from other genera by the two unequal valves of its dehiscent fruits. In northwestern North America, there are three taxa of *Tiarella* which have traditionally been separated into species on the basis of "consistent" differences in leaf morphology. Hitchcock *et al.* (1961) stated that "with one exception" there appears to be no intergradation of leaf patterns among the three taxa, even in sympatric populations. They therefore favored the retention of the three taxa as distinct species, *T. trifoliata, T. unifoliata,* and *T. laciniata,* as was proposed by Lakela (1937).

However, intermediate leaf forms have been observed, both in the present study and earlier. Kern (1964, 1966) showed that when the areas of distribution overlap, as they frequently do, intergradient forms are evident. In addition to noting and collecting intergradient plants, Kern hybridized the three taxa under greenhouse conditions; and all cross pollinations resulted in the production of seeds which although not germinated "appeared" to be viable. She recognized the three taxa as comprising one "species complex," *T. trifoliata,* with two subspecies, ssp. *unifoliata* and ssp. *trifoliata,* the latter with two varieties, var. *trifoliata* and var. *laciniata.* For *convenience* of discussion in this paper, the three taxa have been treated as species.

The three species occupy similar ecological niches—moist organic soils of mature coniferous forests—in which they are associated with various shrubs, dicotyledonous herbs, ferns, and cryptogams. In spite of the apparent close similarity of ecological requirements, there is some altitudinal separation of at least two of the species, *T. trifoliata* and *T. unifoliata,* which under allopatric conditions retain their integrity. The distribution of the species is considered in this paper in conjunction with the vegetation classification of Franklin and Dyrness (1969) who recognize four vegetative zones in western Washington. These include the *Picea sitchensis* (sitka spruce) Zone, coastal in distribution; the *Tsuga heterophylla* (western hemlock) Zone, extending from near sea level to an upper limit of approximately 3500 feet; the *Abies amabilis* (silver fir) Zone, extending upward from the *Tsuga heterophylla* Zone to approximately 4500 feet; and the *Tsuga mertensiana* (mountain hemlock) Zone, extending from the *Abies amabilis* Zone to the timberline. The altitudinal limits of these zones vary considerably and are determined by slope and other environmental factors.

Tiarella laciniata, characterized by its divided leaves (Fig. 1), is primarily restricted to the coastal *Picea sitchensis* Zone but is frequently found in the *Tsuga heterophylla* Zone and occasionally in the *Abies amabilis* Zone. According to Kern (1966) it is always found sympatrically with *T. trifoliata* with which it intergrades freely.

Tiarella trifoliata, characterized by its trifoliate leaves (Fig. 2), is a conspicuous understory associate in moist areas of the *Picea sitchensis* and *Tsuga heterophylla* Zones. However, it has been observed by the author to occur well upward into the *Abies amabilis* Zone at elevations as high as 4500 feet.

Figure 1. *Tiarella laciniata* Hook.

Tiarella unifoliata, characterized by simple leaves (Fig. 3), is most common in the understory of the upper regions of the *Tsuga heterophylla* Zone extending upward through the *Abies amabilis* Zone into the *Tsuga mertensiana* Zone and downward to well below 1000 feet.

From the above discussion it becomes obvious that there can be extensive overlap in the distribution of the three taxa. The site from which the specimens were taken in the present study was a mature forest in the *Abies amabilis* Zone. *Tiarella trifoliata* and *T. unifoliata* appeared to occur with approximately equal frequencies; *T. laciniata* was less common. All stages of intermediates were observed, particularly between *T. trifoliata* and *T. laciniata* and between *T. trifoliata* and *T. unifoliata.*

Materials and Methods

All experimental plants were collected in an area along the Racehorse Creek drainage above Welcome, Washington, Whatcom County, at an elevation between 2700 and 2900 feet. Two collections of 80 plants each were made, one on July 13, 1969, the other on August 10, 1969. On both occasions an attempt was made to collect plants representative of the three typical forms and all stages of intermediacy.

Photographic copies were made of basal leaves of all experimental plants and were traced directly in the preparation of illustrations (Figs. 4, 5, 6, 7, 8). After copies had been made, the fresh leaves were extracted in methanol-hydrochloric acid, 99:1 v/v, over a period of several days at 5°C. The crude extracts were then concentrated and spoted on sheets of Whatman #3MM filter paper (46 cm x 57 cm) and developed by

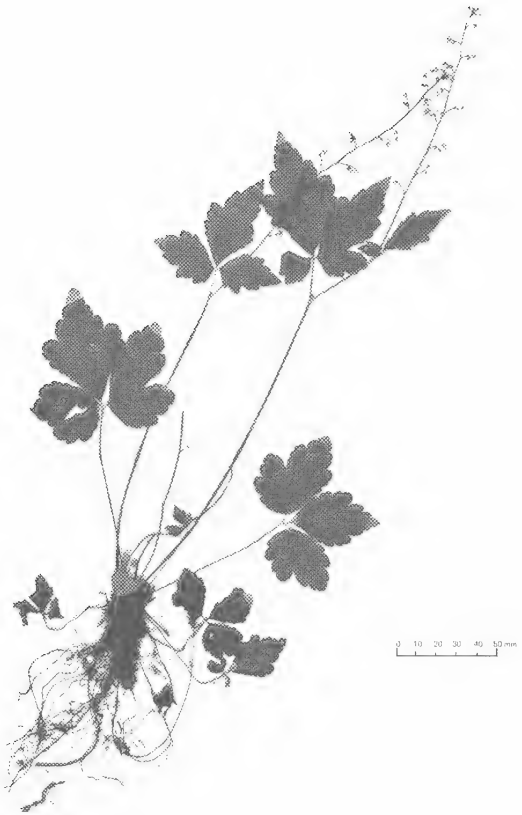


Figure 2. *Tiarella trifoliata* L.

descending, two dimensional chromatography. The first directional solvent was n-butanol-acetic acid-water (BAW), 62:12:26 v/v/v, the second was 15 per cent acetic acid. The chromatograms were observed over a u.v. lamp and the spots were characterized according to their R_f values and physical appearance, before and after having been exposed to ammonia vapor. Color properties and R_f values of the pigment spots are presented in Table 1. No attempts were made to identify the individual pigments.

Similarities of individual plants were determined by means of computer-assisted comparative analyses of pigment profiles, applying the techniques established by Sokal and Sneath (1963) and Sokal (1966), and employed by Taylor and Campbell (1969). The measure of similarity (similarity index value or s-value) between two species was derived using the formula:

$$s = \frac{\text{similarities}}{\text{similarities} + \text{dissimilarities.}}$$

A similarity would be the common occurrence of a pigment in the two plants being considered; a dissimilarity would result from the occurrence of a pigment in one of the plants and not in the other. A pigment not occurring in either of the plants was

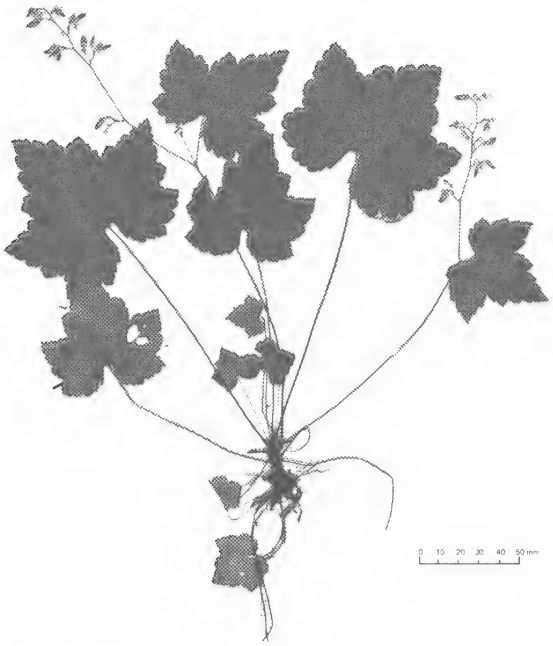


Figure 3. *Tiarella unifoliata* Hook.

not considered in the determination of similarity. The s-values were determined for all combinations of individual plants, and the plants were "clustered" accordingly by the computer.

All experimental plants were collected during anthesis, and pollen fertility determinations were made on the basis of stainability of pollen grains in acetocarmine. A minimum count of 500 pollen grains, including fertile (plump and well stained) and sterile grains, was made from each plant. From these figures, the percentage of fertility was calculated. The mean percentage of fertility and its standard deviation were determined for each of the three species and for each type of intermediate. These data were statistically analyzed.

Results

From field observations it has become obvious that the only phenotypic character, leaf morphology, by which the three species of *Tiarella* can be separated loses its consistency in sympatric populations and variation in lobing is continuous. Figures 4, 5, and 6 show the three combinations of species together with various intermediate forms. Figures 7 and 8 show the extent of variation which freqently occurs in a single, mature "hybrid" plant.

In view of the paucity of visible distinguishing characteristics, and in order to assess better the relationships of the three species, chromatographic separation and characterization of phenolic pigments was employed. A total of 55 pigments were characterized (Table 1) and their distribution among experimental plants was recorded. It was naturally assumed that if there were extensive genetic differences among the species, these would be reflected in the pigment distribution. It was further assumed that if the

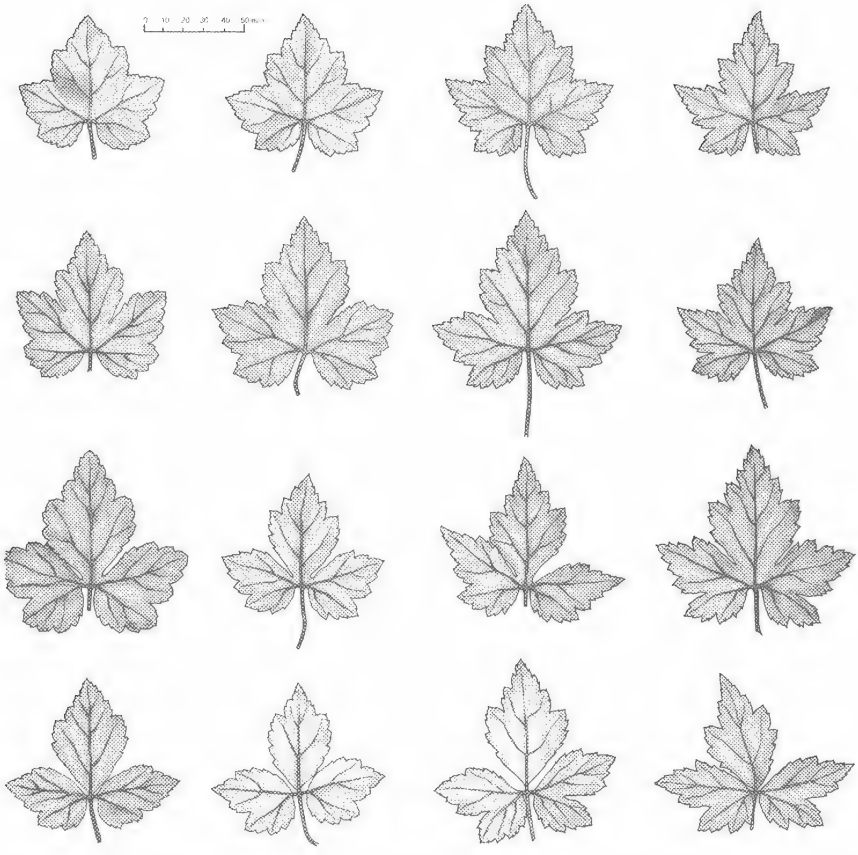


Figure 4. Basal leaves from individual plants of the species *Tiarella unifoliata* (top row) and *T. trifoliata* (bottom row) and of intermediate forms. Interspecific variation or intergradation is represented along the vertical and diagonal planes; intraspecific variation is represented along a horizontal plane.

plants with intermediate leaf-lobing patterns were hybrids, they would have pigment profiles representative of both parental species. The cluster analysis (Table 2) failed to show any systematic grouping of taxa based on pigment similarities. In order to test the hypothesis that there were no phenolic differences among the species, the *mean* similarity values of plants within each of the species and intermediate groups were determined and statistically compared to those of each combination of species and intermediates (Table 3). At the 95 percent confidence level, there was no difference among any of the means. Of course, if the species can not be separately characterized chromatographically, hybrids can not be identified.

Although there was no distinction among the pigment profiles of the species, in the computer analysis there was complete separation of the plants collected in July from those collected in August. This is shown in Table 2, the upper group of plants having been collected in July, the lower group in August. The significance of this "environmentally" induced variation is discussed elsewhere.

The degree of genetic similarity among species can also be reflected in the pollen

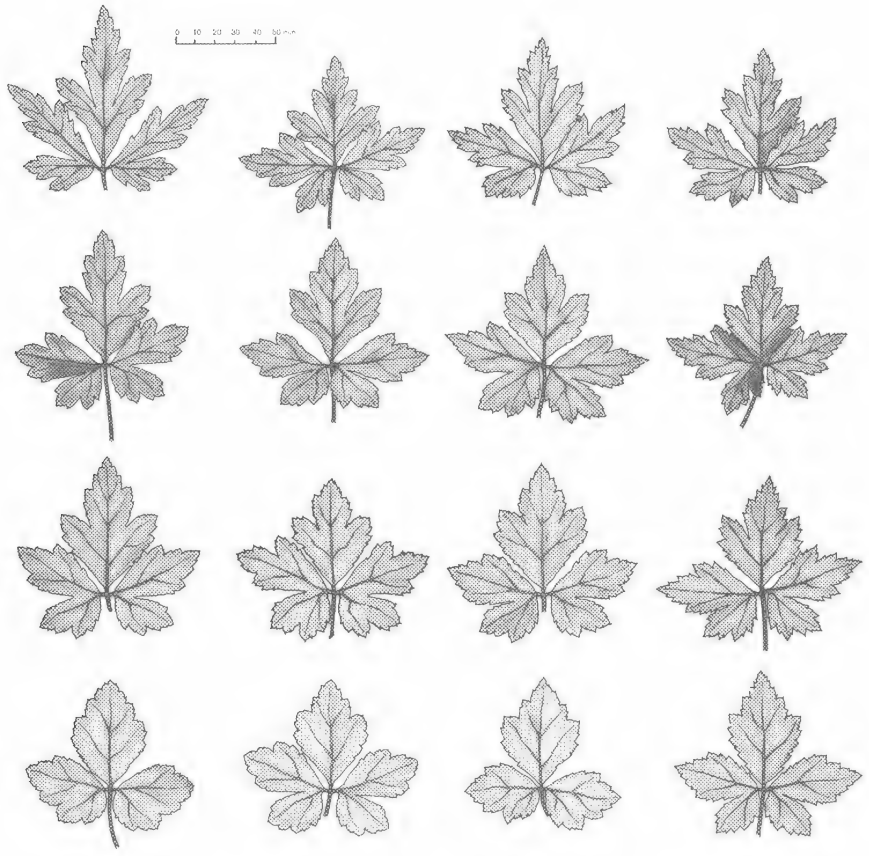


Figure 5. Basal leaves from individual plants of the species *Tiarella laciniata* (top row) and *T. trifoliata* (bottom row) and of intermediate forms. Interspecific variation or intergradation is represented along the vertical and diagonal planes; intraspecific variation is represented along a horizontal plane.

fertility of the hybrids. In this study, there was very little distinction between the pollen fertility of the *Tiarella* species and "hybrids" (Table 3), and the differences were not significant at any level.

Discussion

All the results of this study, coupled with those of Kern (1964), indicate that except for convenience there is no *apparent* basis for the division of the western North American representatives of *Tiarella* into separate taxa at the specific or subspecific level. However, the fact that the three taxa continue to be differentiated along an altitudinal gradient and in sympatric populations, albeit incompletely so, suggests that breeding behavior and/or ecotypic distinctions are instrumental in preventing complete convergence. It has recently been suggested (Ehrlich and Raven, 1969) that breeding patterns are such that gene flow is much more restricted in populations than had previously been suspected. Limited gene flow would help to maintain the integrity of *Tiarella* species even when occurring sympatrically. Furthermore, in populations

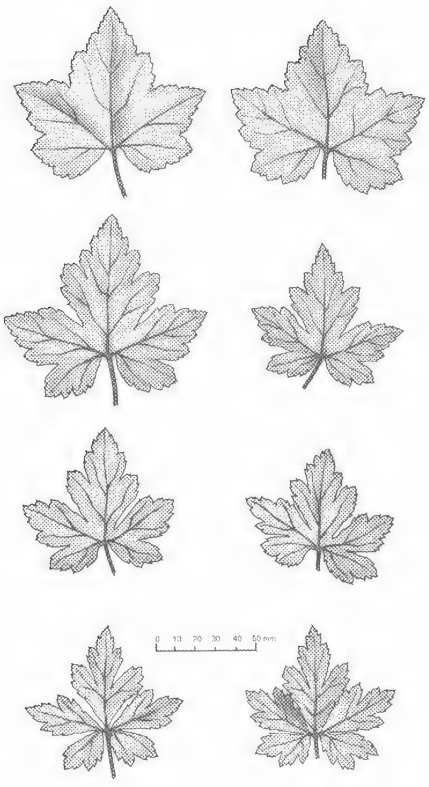
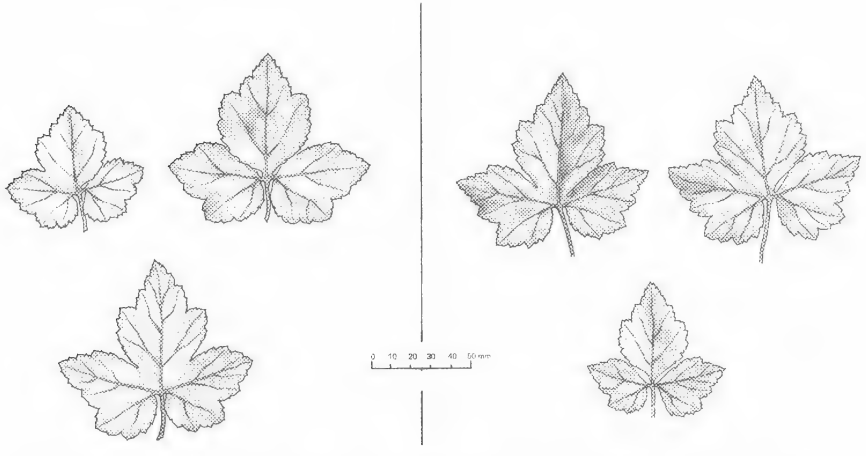


Figure 6. Basal leaves from individual plants of the species *Tiarella unifoliata* (top row) and *T. laciniata* (bottom row) and of intermediate forms. Interspecific variation or intergradation is represented along the vertical plane; intraspecific variation is represented along the horizontal plane.



Figures 7 and 8. Intraindividual variation of basal leaves occasionally occurring in "hybrid" plants. (*T. trifoliata* x *T. unifoliata*).

TABLE 1. Pigment properties and occurrence.

Pigment	Rf Values (x 100) BAW[2]	15%AC[3]	UV	UV + NH_3	Visible	Vis + NH_3	Frequency of occurrence[4]
01	50	17	YFl	b.YFl	—	f.Y	.5987
02	42	11	p.YFl	YFl	—	—	.7105
03	38	03	p.YFl	YFl	—	—	.7237
04	50	37	f.YFl	p.YFl	—	—	.3684
05	66	15	p.YFl	b.YFl	—	f.Y	.5461
06	67	02	p.YFl	b.YFl	—	f.Y	.6053
07	81	03	YFl	b.YFl	—	f.Y	.4276
08	19	03	YOFl	b.Y-OFl	—	—	1.0000
09	31	51	d.BrAb	YFl	—	Y	1.0000
10	40	59	d.BrAb	Y-BrAb	—	Y	1.0000
11	66	60	BFl	b.B-GFl	—	—	1.0000
12	70	18	Br-BlAb	BrBlAb	—	—	1.0000
13	73	24	Br-BlAb	Br-BlAb	—	—	1.0000
14	87	61	BFl	v.b.B-HFl	—	—	.9605
15	93	68	WBFl	v.b.BFl	—	—	.6645
16	94	80	dk.BFl	b.BFl	—	—	.4408
17	82	83	———	Y-GFl	—	—	.8158
18	76	73	WBFl	b.B-GFl	—	—	.8553
19	81	88	dk.B Ab	v.b.BFl	—	—	1.0000
20	78	80	BFl	v.b.B-GFl	—	—	.9803
21	69	77	BFl	v.b.B-GFl	—	—	1.0000
22	22	43	d.BrAb	p.YFl	—	—	.9934
23	32	68	d.BrAb	d.BrAb	—	—	.8224
24	45	75	p.BFl	B-GFl	—	—	.9605
25	78	46	p.BFl	B-GFl	—	—	.6184
26	82	33	p.BFl	B-GFl	—	—	.5855
27	43	83	———	WB-GFl	—	—	.0789
28	08	72	YFl	YFl	—	—	.5132
29	38	72	———	dk.Bfl	—	—	.6382
30	49	78	———	dk.BFl	—	—	.5000
31	77	66	w.Ab	PuFl	—	—	.2566
32	51	63	d.BrAb	Y-BrAb	—	f.Y	.5395
33	24	58	d.Br-BlAb	d.Br-BlAb	—	—	.2039
34	27	08	f.YFl	p.YFl	—	—	.4013
35	70	51	d.BrAb	Y-BrAb	—	—	.3750
36	86	45	———	p.B-GFl	—	—	.3421
37	40	34	d.BrAb	b.Y-OFl	—	Y	.9605
38	88	79	B-GFl	b.B-GFl	—	—	.2566
39	61	47	d.BrAb	Y-BAb	—	f.Y	.5066
40	61	61	dk.BrAb	Y-BAb	—	—	.0461
41	35	83	———	p.BFl	—	—	.0724
42	51	21	f.YFl	f.YFl	—	—	.0329
43	68	38	f.YFl	Yfl	—	—	.3158
44	09	04	b.YFl	b.YFl	—	—	.3553
45	52	30	p.Y-BrFl	d.BFl	—	—	.5066
46	78	58	———	p.Y-GFl	—	—	.4013
47	25	76	———	bk.BFl	—	—	.4211
48	28	21	d.R	B	R	B	.0066
49	31	10	d.R	B	R	B	.0329
50	11	65	d.BrAb	YFl	—	—	.1842
51	91	73	f.B-GFl	Y-GFl	—	—	.4145
52	42	50	d.YFl	d.Y-BrFl	—	—	.4342
53	76	74	———	b.BFl	—	—	.1382
54	27	41	d.R	B	R	B	.0724
55	63	25	———	w.B-GFl	—	—	.1513

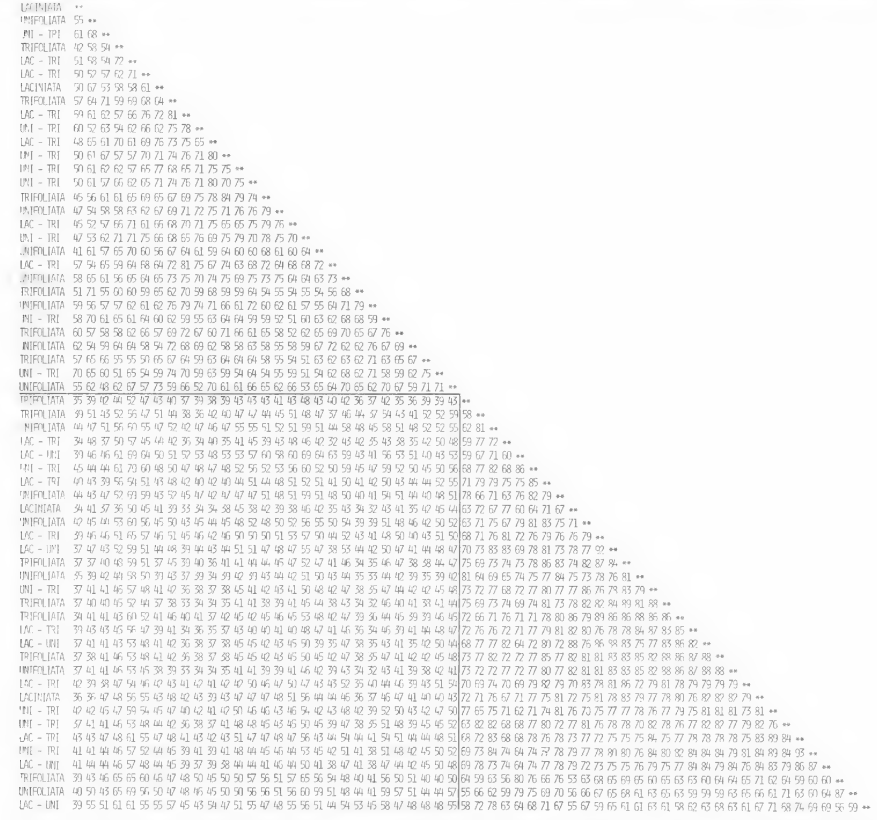
[1] KEY: b. = bright, v.b. = very bright, d. = dull, dk. = dark, f. = faint, p. = pale, w. = weak, B = blue, Bl = black, Br = brown, G = green, O = orange, R = red anthocyanin's, Y = yellow, Ab = absorption, Fl = fluorescent.

[2] n-butanol-acetic acid-water, 62:12:26 v/v/v.

[3] 15% acetic acid.

[4] The proportion of individual plants in which the pigments were found.

TABLE 2. Abbreviated[1] cluster analysis of sample specimens.



[1] For convenience of illustration, less than one fifth of all experimental plants are shown in this analysis. Representative plants were selected at regular vertical intervals from the original computer analysis insuring that all plants shown here are in their proper relative position.

TABLE 3. Mean pigment similarities (s-values) and pollen fertilities.

Species and intermediates	Means s-values[1] and standard deviations within and between species and intermediate groups						Mean pollen fertilities and standard deviation	Sample size (no. of plants)
	laciniata	*trifoliata*	*unifoliata*	*lac-tri*	*lac-uni*	*tri-uni*		
laciniata	69[2]						97[2]	6
trifoliata	67±12.1	68±9.9					96±2.9	38
unifoliata	66±10.8	67±9.9	68±8.4				95±3.3	36
lac-tri	67±11.3	70±9.6	69±11.3	72±6.2			95±4.0	32
lac-uni	67±10.7	66±9.4	66±10.7	68±9.5	66±9.8		94±4.3	10
tri-uni	68±10.4	68±13.3	69±12.4	67±12.2	69±11.6	71±9.4	95±3.5	38

[1] These values are the average of the individual means *within* the July and August collections, *i.e.,* similarity values *between* individuals collected in July and those collected in August were not included in these calculations.

[2] Standard deviations were not determined due to the small sample size.

where phenotypic intergradation is common, the proportion of typical forms to intermediate forms is high (Kern, 1966), suggesting selective breeding behavior or differential survival of progeny or both. Finally, the continuous variation in the pattern of leaf-lobing strongly suggests the involvement of multiple genes; and if there were random breeding, nonselection, and nonlinkage of the genes involved, the typical (extreme) forms would be the exception rather than the rule.

It is unlikely that the retention of distinct taxa is entirely dependent upon breeding behavior. The problem arises, however, in trying to correlate the pattern of leaf-lobing with its adaptive significance. Experimental studies by Sakai (1961) have shown that there is very little correlation between the general form of a plant and its ability to compete. Such may be the case in *Tiarella, i.e.,* the leaf pattern may be incidental or possibly linked to adaptive genes. Yet, the existence of extensive leaf variation suggests that there must be—or was at one time—differential selection for variants produced from the simple leaves of *T. unifoliata,* presumed to be the most primitive of the three species on the basis of wider distribution and greater similarity to closely related genera, *e.g., Heuchera.* Also, the general trend is toward derivation of compound leaves from simple leaves (Cronquist, 1968), although the converse may be true (Stebbins, 1967).

Tiarella may represent a polymorphic species with the extreme forms maintaining some selective advantage under prescribed environmental conditions. This is a hypothesis difficult to test for two reasons: 1) It is difficult to recognize any distinction among natural habitats of the three taxa, even when growing apart; therefore, it cannot be said that the species utilize different environmental resources. If they are similar in their requirements, there is no evidence that a plant of one leaf form would have a selective advantage over that of another. 2) In sympatric populations, intergradient forms are common, appear successful, have equally high pollen fertility, and set seeds regularly. In any case, if the three taxa represent ecotypes there is no apparent correlation between physiological differentiation associated with ecological specialization and morphological and chemical characteristics.

Finally, the altitudinal distribution of the species may be a reflection of their response to associated members of their community, the structure of which changes with increased altitude.

In order to ascertain if there are different fitness coefficients among the three species in relation to environmental variation along an altitudinal gradient, extensive ecological studies and/or transplant experiments are necessary. Such experimentation was not a part of the present study which was designed to test the degree of similarity of the species of *Tiarella.*

Literature Cited

Cronquist, A. 1968. The evolution and classification of flowering plants. Houghton Mifflin Company, Boston, Mass.

Ehrlich, P. R., and P. H. Raven. 1969. Differentiation of populations. Sci., 165:1228-1232.

Franklin, J. F., and C. T. Dyrness. 1969. Vegetation of Oregon and Washington. U.S.D.A. Forest Service Research Paper PNW 80.

Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1961. Vascular plants of the Pacific Northwest, Vol. 3. University of Washington Press, Seattle, Washington. pp. 59-61.

Kern, P. 1964. A taxonomic revision of the genus *Tiarella.* Masters degree thesis (unpublished). University of Washington, Seattle.

———. 1966. The genus *Tiarella* in western North America. Madrono, 18:152-160.

Lakela, O. 1937. A monograph of the genus *Tiarella* in North America. Amer. Jour. Bot., 24: 344-351.

Sakai, K. I. 1961. Competitive ability in plants: Its inheritance and some related problems. Symp. Soc. Expl. Biol., 15:245-263.

Sokal, R. R. 1966. Numerical taxonomy. Sci. Amer., Dec. pp. 106-116.
Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco, California.
Stebbins, G. L. 1967. Adaptive radiation and trends of evolution in higher plants. In Dobzhansky, T., M. K. Hecht, and W. C. Steare, Eds. Evolutionary Biology I, pp. 101-140. Appleton-Century-Crofts, New York.
Taylor, R. J., and D. Campbell. 1969. Biochemical systematics and phylogenetic interpretations in the genus *Aquilegia.* Evolution, 23:153-162.

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Distribution and Growth of Indigenous Fluvial and Adfluvial Cutthroat Trout (Salmo clarki), St. Joe River, Idaho

Cutthroat trout (*Salmo clarki*) support important sport fisheries in western North America. Anadromous cutthroat migrate from coastal streams to the sea (Sumner, 1962), while inland cutthroat either spend their entire lives in streams as fluvials (Bjornn and Mallet, 1964) or leave the stream system and migrate into lakes as adfluvials (Bjornn, 1961; Cope, 1956; Irving, 1954). Because of its moderately large size the St. Joe River in North Idaho enabled us to explore the characteristics of fluvial and adfluvial cutthroat indigenous to one river system.

We set out to differentiate between fluvial and adfluvial forms of cutthroat on the basis of scale analysis. Scales from lake-run cutthroat have circuli patterns similar to those of sea-run cutthroat described by Sumner (1962). The lake habitat causes the circuli to become heavily embossed and widely separated whereas the stream habitat results in finely textured and narrowly spaced circuli. The scales of fluvial trout lack the lake-formed circuli and appear similar to premigratory juvenile adfluvial cutthroat.

In particular, we investigated timing and duration of spawning activity, migration, distribution, length-age relationships, fry emergence, and early scale development of fluvial and adfluvial cutthroat trout.

Observations and collections of trout were made in 1961, 1962, and 1964 in the St. Joe River mainstream and in Benewah, Thorn, Trout, Mica, Gold, and Simmons Creeks, tributaries which lie near the mouth, mid-river, and headwaters of the St. Joe River. The tributaries were arbitrarily chosen according to their geographical location to the river main stem, for at inception of the study we had no prior knowledge of use of these streams, or any others, by fluvial or adfluvial cutthroats.

The Study Area

The St. Joe River originates on the west side of the Bitterroot Mountains near the Idaho-Montana border (Fig. 1), then flows west to the south end of Coeur d'Alene Lake near St. Maries, Idaho. The lowest 42 km (26 miles) of the river has relatively slight gradient and the water flows slowly because of a rise in water level of Coeur d'Alene Lake resulting from construction of Post Falls Dam in 1906. This rise in water level connects Benewah, Chatcolet, Coeur d'Alene, and Round Lakes. Above the 42-km backwater area the river drops moderately to steeply with occasional flat stretches and deep pools. The lower four study tributaries (Benewah, Thorn, Trout, and Mica Creeks) have relatively high maximum to minimum flow ratios

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compared to those of Gold and Simmons Creeks and the St. Joe River. Magnitude of the flow ratios reflects differences in elevation, type of precipitation, and run-off. The spring run-off occurs later in the season and more gradually at higher elevations.

Methods

A total of 442 cutthroat trout were collected by electrofishing, angling, and netting mature fish during spawning migrations. Immature cutthroat with three or less stream annuli on their scales were classified as juveniles because we could not distinguish between progeny of fluvial and adfluvial parents on the basis of appearance. Mature three-year-old fish and mature and immature older fish were identified as either fluvial or adfluvial on the basis of absence or presence of lake growth on their scales.

The migration class of adfluvial cutthroat was based upon the number of years the trout had spent in the stream environment as juvenile fish. For example, we designated a fish whose scales showed one stream annulus as Migration Class I; if the scales showed two stream annuli, we categorized the fish as Migration Class II. Similar to a generally accepted expression that combines migration class with age at capture in anadromous fishes, we used two numbers, one of which is a subscript. For example, the expression, 3_1, represents a fish of Migration Class I which entered our samples in its third year of life. Such a fish would have spent one year in the stream and two years in the lake environment.

Scales were obtained from an area just above the lateral line below the insertion of the dorsal fin and were magnified 81 times to determine annual growth. Annuli were measured from the focus of the scale to the outer margin or last constricted circulus of the annulus, and circuli were counted between the focus and the first annulus only. Scales on mature cutthroat commonly had eroded along the horizontal radial line which necessitated making measurements from the focus to the annulus along the 20° ventral line described by Clutter and Whitesel (1956).

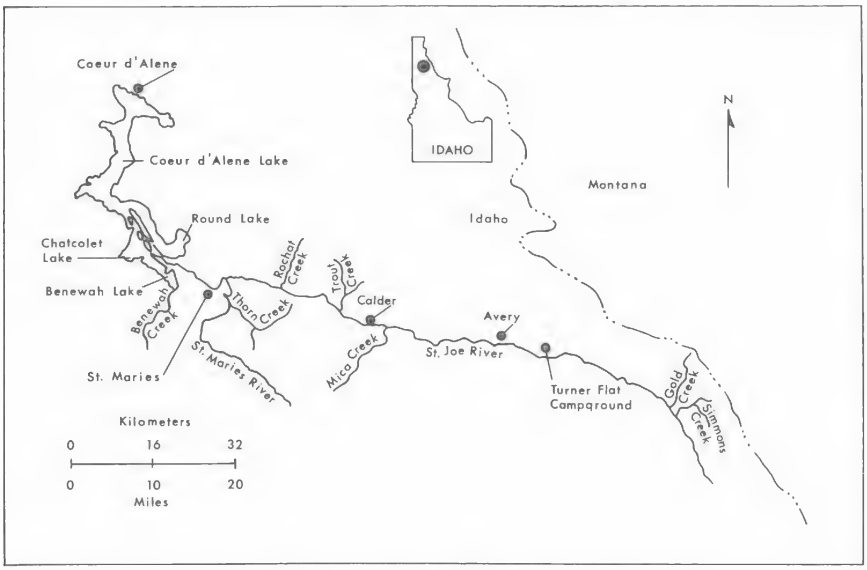

Figure 1. Map of the St. Joe River drainage showing tributary streams sampled.

For back-calculations of fish length, the fork length and length of scale radius along the 20° ventral radial line were plotted on log-log paper (Smith, 1955). The logarithmic means of both parameters were then determined and a 45° line drawn through the intersection means. The data fitted the 45° line well enough to justify simple logarithmic-proportion back-calculation of fish length at each age (Fig. 2).

In Yellowstone Lake, Wyoming, some cutthroat fail to develop scales during their first year of life, resulting in obvious problems in determining age by the scale method (Laakso and Cope, 1956). To determine if the same phenomenon took place with cutthroat in the St. Joe River, the skin from the left side of young-of-the-year fish was carefully removed and stained with Alizarin Red Dye mixed with 0.02 N KOH. As scales stained more intensely than the skin, we could easily observe them under a microscope or on a scale projector.

Results

The migration of mature adult adfluvial cutthroat from the lake complex to streams begins by early April and continues throughout the month. Adfluvial cutthroat with "green" eggs were first caught in Benewah Creek on April 8 and in Thorn Creek on April 15, 1962. From May 2 to 22, 1964, fertile eggs were stripped from all of 24 female adfluvials held captive in pens in Thorn Creek. Two ripe, two-year-old, and one ripe, three-year-old, fluvial cutthroat (196 to 201 mm in fork length), with obvious parr marks, were also captured in Thorn Creek on May 16, 1964.

The upstream migration limit of adfluvial cutthroat in the St. Joe River was not determined with certainty. In June 1961, four adfluvial fish were caught in the vicinity of the Turner Flat Campground area, 121 km (75 miles) upriver from Coeur d'Alene Lake. Above this area, five fluvial fish were collected.

Although a post-spawning migration to the lake complex was not observed from any of the tributary streams, catch records showed that anglers commonly have caught spent fish in the lower river in early June and occasionally in late July.

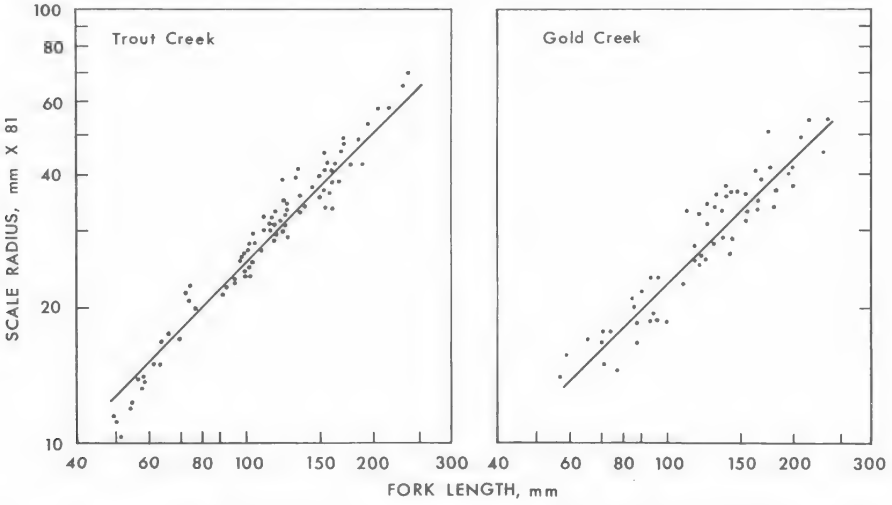

Figure 2. Body-scale relationships of cutthroat trout from Trout and Gold Creeks. Solid line of 45° drawn through the intersection of the logarithmic means of the fork length and the length of the ventral 20° scale radius.

Of 117 adfluvial cutthroat captured in the St. Joe River, Benewah, and Thorn Creeks, 50 per cent were classed migration-age group 4_2, 71 per cent as four-year-old at maturity, and 62 per cent as having spent two years in the lake complex prior to spawning (Table 1). As for migration classes, 7 per cent of the adfluvials had

TABLE 1. Migration-age frequency of 117 adfluvial cutthroat from the St. Joe River drainage.

	Migration-age designation						
Stream	3_1	4_1	3_2	4_2	5_2	4_3	5_3
Benewah Creek	0	4	0	9	0	0	0
Thorn Creek	5	4	4	20	2	1	1
St. Joe River	7	11	6	29	8	5	1
Total	12	19	10	58	10	6	2
Per cent of total	10.3	16.2	8.5	49.6	8.5	5.1	1.7
Mean fork length (millimeters)	240	300	228	323	366	260	325

spent one year; 67 per cent, two years; and 26 per cent, three years in the stream environment. In contrast, Bjornn (1961) determined by scale analysis of mature cutthroat from Priest Lake, North Idaho, that 0 per cent of the adfluvials had spent one year; 38 per cent, two years; 57 per cent, three years; and 5 per cent, four years in tributaries as juveniles.

Mean fork lengths of adfluvial cutthroat aged three (22 fish), four (83 fish), and five (12 fish) were 235, 313, and 359 mm, respectively. Mean fork lengths of adfluvial cutthroat that resided one year (16 fish), two years (72 fish), and three years (29 fish) in the lake before returning to the river were 240, 309, and 323 mm, respectively.

After adfluvial cutthroat entered the lake environment, their growth rate accelerated (Fig. 3) and we could recognize some cutthroat captured in creeks as adfluvials by their large size, because all cutthroat over 300 mm in length showed lake growth on their scales. A decline in growth occurs during the year prior to spawning, perhaps because gonadal development requires food energy otherwise available for body protein or because the metabolic rate of trout increases prior to the spawning period (Beamish, 1964).

Emergent fry were first observed in Thorn Creek on June 11, 1962. By June 20 many newly emerged fry were captured in all of the lower four tributary streams. In Gold and Simmons Creeks, fry emergence was not observed until early August, although turbidity due to rapid snow melt limited visibility in these two streams.

Scales from Benewah, Thorn, and Gold Creek fry first developed on the caudal peduncle in the region of the lateral line, an area similar to that on cutthroat trout from Yellowstone Lake, Wyoming (Brown and Bailey, 1952). However, the St. Joe fry lacked the independent patches of developing scales noted on the skin of Yellowstone fish at other locations.

Fry from Benewah and Thorn Creeks developed scales as early as July, but those from Gold Creek, not until September. The smallest fish with scales in Benewah Creek measured 42 mm; in Thorn Creek, 45 mm; and in Gold Creek, 46 mm. Actual fish length at the time of initial scale development fell short of the above measurements because the fish examined had already formed some scales. In mid-

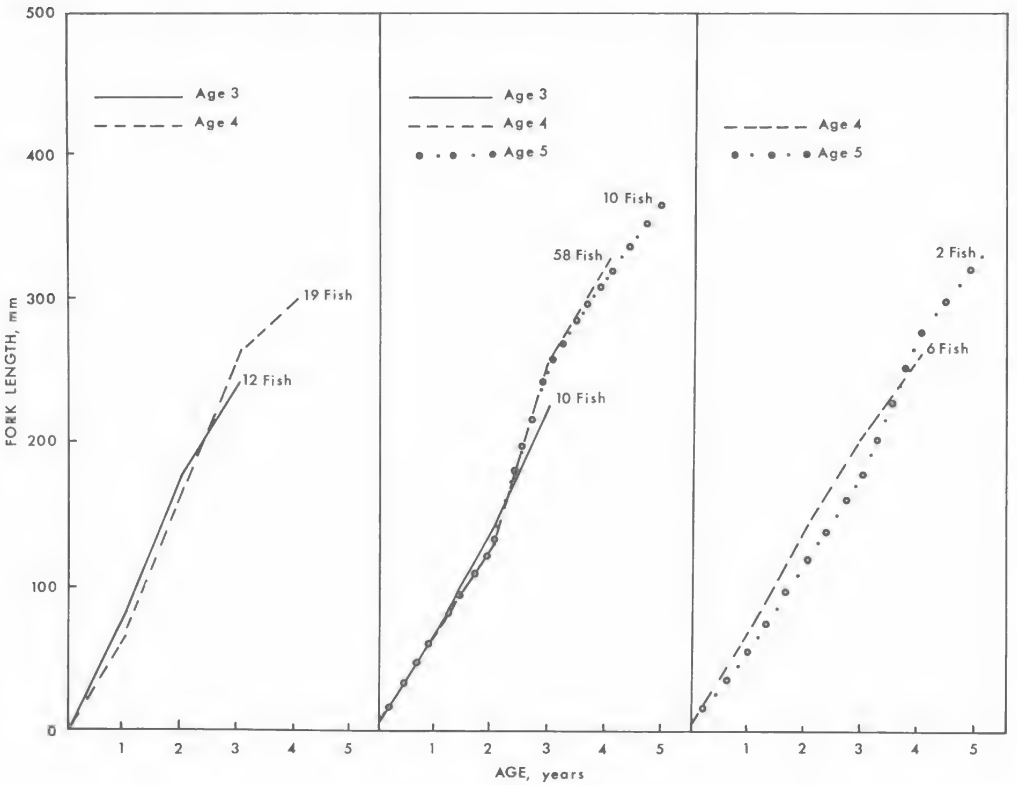

Figure 3. Age-length relationships of adfluvial cutthroat trout, St. Joe River, Idaho.

September, 30 cutthroat fry captured in Gold Creek ranged from 30 to 52 mm in fork length, but only those greater than 46 mm had developed scales.

Annulus formation on cutthroat scales takes place in the spring. A sexually immature cutthroat was captured in the lake complex on May 20, 1962, just completing a second annulus. The scales from this fish showed two years of stream growth but no lake-formed circuli; presumably the fish had just entered the lake complex when caught. Scales from a 4_2 cutthroat captured in Thorn Creek on April 25, and a 4_2 fish captured near the mouth of the St. Joe River on May 10, 1962, were also in the process of forming annuli. The scales from all fish captured in June and July had one or more circuli beyond the last annulus.

Although we cannot draw firm conclusions from our data on scale formation, cutthroat seem to spawn later in upper tributaries, and fish hatched in these streams may not possess a full complement of scales at the end of the growing season. As the scales of young-of-the-year cutthroat from Gold and Simmons Creeks deposit few circuli by spring, scales could in some years either lack first-year annuli, contain poorly defined ones, or have a mixture of both conditions in samples containing several year classes.

Heavy angling pressure in recent years prevented us from collecting any large fluvial cutthroat from Gold or Simmons Creeks. However, Bachmann (1958) reported that Age Class I cutthroat with some summer growth averaged 140 mm in total length, whereas our fish at completion of the first-year annulus averaged 50 mm in fork length. This large discrepancy suggests that Bachmann counted only those annuli present on the scales and did not consider the possibility that some initial annuli were missing or unrecognizable. By adjusting Bachmann's length data, we find considerable agreement between the two studies. Gold Creek fluvial cutthroat in their third, fourth, and fifth growing season averaged 139 mm (9 fish), 165 mm (2 fish), and 208 mm (3 fish) in total length, respectively; Simmons Creek fluvial cutthroat in their third, fourth, fifth, and sixth growing season averaged 142 mm (16 fish), 193 mm (108 fish), 223 mm (12 fish), and 277 mm (7 fish) in total length, respectively. Allowing for the difference between fork and total lengths, Bachmann's 139 and 142 mm means for total length adjusted to the third growing season (Age Class II) correspond closely with our 145 mm mean (Table 2) for juveniles at third annulus formation.

TABLE 2. Calculated mean fork length for stream growth of mature adfluvial and juvenile cutthroat trout in the St. Joe River system. Sample size in parentheses.

	Fork length, millimeters		
Age class	Mature adfluvials	Juveniles[1]	Juveniles[2]
I	69 (90)	68 (195)	50 (118)
II	135 (65)	128 (37)	98 (98)
III	206 (6)	215 (9)	145 (73)

[1] Includes Benewah, Thorn, Trout, and Mica Creeks and the St. Joe River.
[2] Includes Gold and Simmons Creeks.

In our scale analysis juvenile cutthroat captured in the lower four study tributaries and the St. Joe River grew at a rate similar to that of adfluvial trout (Table 2). In contrast, juvenile cutthroat in Gold and Simmons Creeks grew much more slowly

than adfluvial trout. We infer that adfluvial cutthroat originate not in the upper tributaries, but in the lower tributaries of the St. Joe River.

Juveniles and adfluvial cutthroat captured in the St. Joe River and the lower four tributaries (Table 3) had almost the same mean lengths at completion of the first annulus and almost the same mean number of circuli within the first annulus. Cutthroat captured in Gold and Simmons Creeks had a much lower mean length at completion of the first-year annulus, and only about one-half as many included circuli as fish from the lower streams.

To test the significance of the differences among the means for fish length at first annulus formation and the included circuli, we assessed the shortest significant ranges using a modification of Duncan's Multiple Range Test (Kramer, 1957) to permit use of unequal sample sizes. In length at first annulus and number of circuli

TABLE 3. Mean length of cutthroat trout at first annulus formation and mean number of circuli within the first annulus for mature adfluvials and fluvial or adfluvial juveniles of the St. Joe River drainage.

Fish type	Sample size	Fork length (millimeters)	Number of circuli
St. Joe juvenile	12	69.2	8.7
St. Joe adfluvial adult	67	69.9	8.3
Benewah Creek juvenile	27	74.2	8.4
Benewah Creek adfluvial adult	13	68.0	8.3
Thorn Creek juvenile	10	66.7	8.5
Thorn Creek adfluvial adult	10	66.1	8.8
Trout Creek juvenile	90	65.9	8.4
Mica Creek juvenile	68	66.6	8.7
Gold Creek juvenile	62	50.4	4.4
Simmons Creek juvenile	53	49.0	3.9

within the first annulus, cutthroat from the lower four tributary streams and the St. Joe River significantly differed from those in Gold and Simmons Creeks ($P<0.01$). The similarity of mean length at first annulus and of the included circuli for the lower four tributaries indicates a comparable environment for growth in these streams.

Discussion

We base our belief that adfluvial cutthroat originate essentially in the lower tributaries and possibly in the mainstem of the St. Joe River on differences in the body length of fluvial and adfluvial fish at the completion of the first-year annulus and the number of circuli within the first annulus. In addition, no adfluvial cutthroat were recorded above the Turner Flat Campground on the St. Joe River.

Although adfluvial cutthroat occupy the lower tributaries, fluvial cutthroat also reside in these streams, especially above falls impassable to upstream migrating adfluvial trout (MacPhee, 1966). Thus, two groups of fish are recognized by behavioral rather than morphological differences. The two groups may live in the same stream areas during their early life, but thereafter, the adfluvial group moves downstream to the lake complex.

To call the fluvial and adfluvial groups of cutthroat distinct races as defined by Dobzhansky (1951) would require a knowledge that either their times or areas of spawning do not overlap. Averett and Espinosa (1968) reported such a situation

for kokanee salmon (*Oncorhynchus nerka*) in Odell Lake, Oregon. If time or location of spawning does overlap in the St. Joe drainage, considerable interbreeding of fluvial and adfluvial cutthroat could occur where barriers (temperature, temporal, or physical) do not interfere.

Mature fluvial cutthroat above falls and other impassable barriers bear conspicuous parr marks (MacPhee, 1969). Mature adfluvial cutthroat have no such marks. Carl *et al.* (1959) picture parr marks on a mature, dwarf, headwater form of rainbow trout (*Salmo gairdneri*). Such dwarf rainbows, up to at least 250 mm in length, occur in abundance above impassable falls in the Halfway River, Upper Arrow Lake, British Columbia.

In the main stem of the Middle Fork of the Salmon River, mature fluvial cutthroat do not have parr marks. Presumably, Middle Fork cutthroat "smolt" in side tributaries and migrate to the main stem where they mature. A large number of these maturing trout migrate seasonally downstream to winter in deep pools in the lower Middle Fork and main Salmon River (Bjornn and Mallet, 1964). Such migratory behavior makes us suspect that some trout originating in the headwaters and side tributaries of the St. Joe River might migrate into the main stem without continuing downstream into the lake.

The possibility exists that some fluvial trout captured in the main stem of the St. Joe River might have heavily embossed and widely spaced circuli on their scales similar to those of fish from the lake environment. Although a small sample of fluvials from the main stem of the St. Joe River (12 fish) did not have lake-type scales, the three mature fluvial cutthroat with parr marks from Thorn Creek had scales with heavily embossed, widely spaced circuli in their second year of life. These fish may have spent their second summer in the river or lake and then returned to the creek.

The possibility is slight that heavily embossed circuli on main stem fluvial fish, if such occurs, could have resulted in wrongly classifying a trout as adfluvial. Ninety per cent of the fish in our samples were captured during the spawning runs in Thorn and Benewah Creeks or in the St. Joe River downstream from Mica Creek. These areas contain few large cutthroat during low summer flows and high water temperatures. On August 10, 1967, skin divers drifting downsteam counted only two cutthroat per mile in about a 30-foot wide visual path in the St. Joe River between Mica Creek and St. Joe City. Most main stem fluvial cutthroat trout occur upstream from Avery in the summer.

The migratory behavior of adfluvial cutthroat parallels that of Kamloops trout, which is characteristically an adfluvial rainbow. Similarly, the coastal cutthroat behave like steelhead migrating to the ocean instead of lakes. Both species of adfluvial and anadromous trout exhibit parr marks as juveniles but not as adults.

Most juvenile sea-run cutthroat in Sand Creek, Oregon, live three to four years in the stream before migrating (Sumner, 1962), a slightly longer time than that found for Priest Lake (Bjornn, 1961) and St. Joe River adfluvial cutthroat. Moreover, the scales from mature sea-run and lake-run cutthroat exhibit at least one stream annulus. This absence of Migration Class 0 suggests that either the juveniles do not leave the stream until "smolting" occurs or that young-of-the-year do not have a high survival rate in lakes or ocean. In contrast, the vast majority of captured adult cutthroat entered Yellowstone Lake, Wyoming as young-of-the-year fish (Laakso and Cope, 1956). Benson (1960) speculated that less-severe competition and predation by larger salmonids on cutthroat fry exist in the lake than in the stream

habitat, which in the absence of other significant predators could account for the high survival of young-of-the-year cutthroat in Yellowstone Lake.

Adfluvial cutthroat grow faster and become larger than the fluvials which remain in the stream environment, providing an obvious enhancement to the fishery in the St. Joe River drainage.

Summary

Adfluvial and fluvial cutthroat trout were studied in the St. Joe River and six streams. Four of the streams were tributary to the St. Joe River and two flowed directly into the Coeur d'Alene Lake complex of which the St. Joe River is a tributary.

The spawning migration of the adfluvial cutthroat from the lake complex to the streams begins in early April. In the St. Joe River adfluvial cutthroat were found as far upstream as 121 km (75 miles). Spent adfluvial cutthroat, apparently returning to the lake complex, are commonly caught by anglers in June and July.

From a total sample of 117 adfluvial cutthroat, 71 per cent were four years old at maturity, and 62 per cent had spent two years in the lake complex prior to spawning.

Stream residence was one year for 7 per cent, two years for 67 per cent, and three years for 26 per cent of the adfluvial fish.

Accelerated growth, as measured by length increase, took place in the lake environment and was clearly evident on the scales of the fish. During the last year of lake residence growth decreased, presumably because of gonadal development.

In the lower tributary streams of the St. Joe River and those tributary to the lake complex, emergent fry were observed in mid-June. In the upper tributaries of the St. Joe River emergence was not until August. Scale development begins when the fish reach about 46 mm fork length.

Juvenile and mature adfluvial cutthroat from the lower tributaries had almost the same mean length at the completion of the first annulus and about the same mean number of circuli within the first annulus. In contrast cutthroat from the upper tributaries had a shorter mean length at completion of the first annulus, and about one-half as many included circuli. This comparison of fish from the upper and lower streams was significantly different ($P<0.01$).

It was concluded that the difference between resident and adfluvial cutthroat in the St. Joe River is behavioral rather than morphological.

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Literature Cited

Averett, R. C., and F. A. Espinosa, Jr. 1968. Site selection and time of spawning by two groups of kokanee in Odell Lake, Oregon. J. Wildl. Mgt., 32(1): 76-81.

Bachmann, R. W. 1958. The ecology of four north Idaho trout streams with reference to the influence of forest road construction. Master of Science Thesis. Univ. of Idaho. xi, 97 pp. (Unpublished).

Beamish, F. W. H. 1964. Seasonal changes in the standard rate of oxygen consumption of fishes. Canad. J. Zool., 42: 189-194.

Benson, N. B. 1960. Factors influencing production of immature cutthroat trout in Arnica Creek, Yellowstone Park. Trans. Am. Fish. Soc., 89(2): 168-175.

Bjornn, T. C. 1961. Harvest, age structure and growth of game fish populations from Priest and Upper Priest Lakes. Trans. Am. Fish. Soc., 90(1): 27-31.

Bjornn, T. C., and J. Mallet. 1964. Movements of planted and wild trout in an Idaho river system. Trans. Am. Fish. Soc., 93(1): 70-76.
Brown, C. J. D., and J. Bailey. 1952. Time and pattern of scale formation in Yellowstone cutthroat trout *Salmo clarkii*. Trans. Am. Microscop. Soc., 80(2): 120-124.
Carl, G. C., W. A. Clemens, and C. C. Lindsey. 1959. The fresh-water fishes of British Columbia. B. C. Provincial Museum, Handbook No. 5, 3rd Ed. 192 pp.
Clutter, R. I., and L. E. Whitesel. 1956. Collection and interpretation of sockeye salmon scales. Int. Pacific Salmon Fish. Comm. Bull., 20: 159 pp.
Cope, O. B. 1956. The choice of spawning sites by cutthroat trout. Proc. Utah Acad. Sci., 34: 73-79.
Dobzhansky, T. 1951. Genetics and the origin of species. Columbia Univ. Press. N. Y. 3rd Ed. 364 pp.
Irving, R. B. 1954. Ecology of the cutthroat trout in Henrys Lake, Idaho. Trans. Am. Fish. Soc., 84: 275-296.
Kramer, C. Y. 1957. Extension of multiple range tests to group correlated adjusted means. Biometrics. 13: 13-18.
Laakso, M., and O. B. Cope. 1956. Age determination in the Yellowstone cutthroat trout by the scale method. J. Wildl. Mgt. 20(2): 138-155.
MacPhee, C. 1966. Influence of differential angling mortality and stream gradient on fish abundance in a trout-sculpin biotope. Trans. Am. Fish. Soc., 95(4): 381-387.
————. 1969. Salmonids: An aquatic product of the forest environment. Coniferous forests of the northern Rocky Mountains: Proceedings of the 1968 Symposium. Sponsored by the Center for Natural Resources, Missoula, University of Montana Foundation, pp. 245-254.
Smith, S. B. 1955. The relationship between scale diameter and body length of kamloops trout, *Salmo gairdneri kamloops*. J. Fish. Res. Bd. Canada, 12(5): 742-753.
Sumner, F. H. 1962. Migration and growth of the coastal cutthroat trout in Tillamook County, Oregon. Trans. Am. Fish. Soc., 91(1): 77-83.

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Grit and Grass: A Historical Geography of Adams County, Washington

Introduction

Between the Rockies and the Cascades, within that vast bowl called the Columbia Basin, lies southeastern Washington, initially shunned by settlers as a desert waste with little future promise. However, enterprising pioneers, eventually relieved of shackling agricultural attitudes, transformed it into a golden granary. Today, life-giving waters flow through reclaimed arid land, and more change is taking place. Diversified crops in irrigated fields appear on the once-barren landscape as man once again alters the land. Change has been a two-way street, however. The land has left its imprint on man and his way of life. The story of Adams County, Washington, is a tale of both—man with his grit and the land with its grass.

The Land

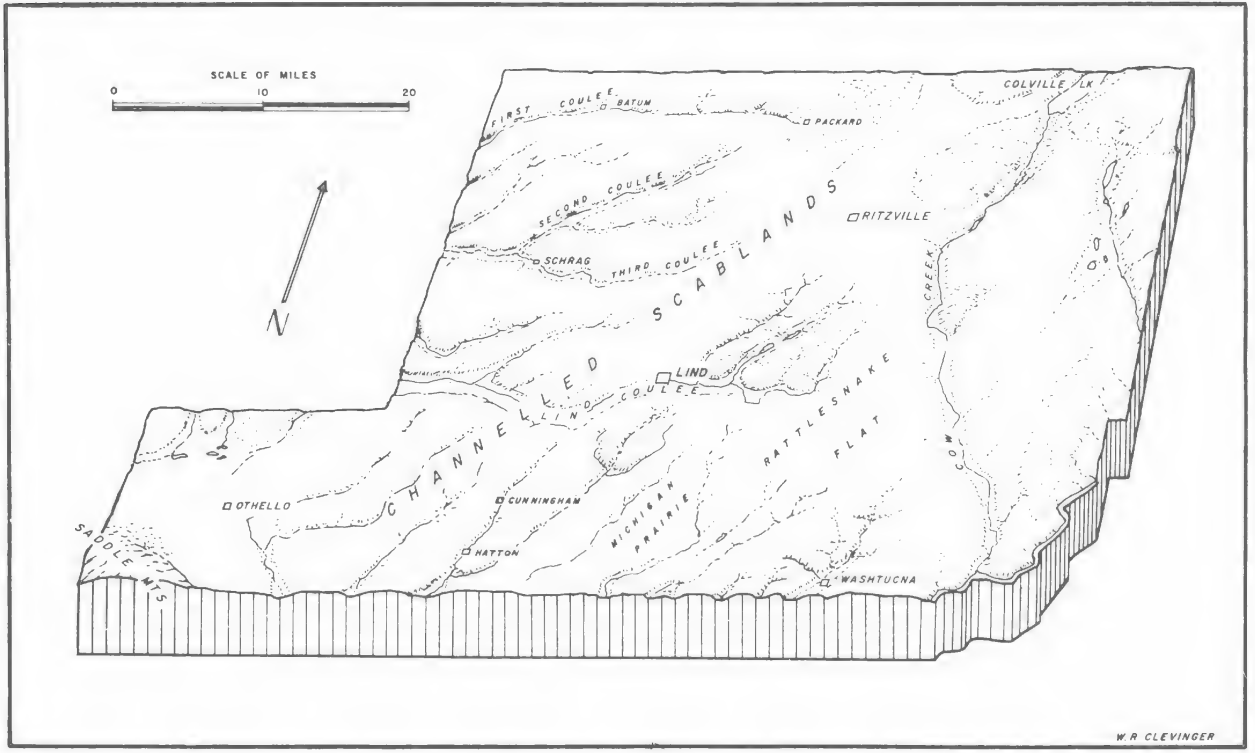
Topography

Although eastern Washington is often assumed to have little or no variation, in fact, between the peaks of the Cascades and the Idaho border there exists a wide variety of topography. The Columbia Plateau comprises much of the region but is far from a tableland. Ghost channels, tilted mesas, giant erratics, steep hills, and deep river valleys relieve monotony, provide a complex landscape, and indicate a varied geologic history.

Although some geologists picture Adams County thirty million years ago as resembling present-day Ferry County, with the Columbia River flowing south through forested hills, the early geologic history lies buried beneath hundreds of feet of lava which erupted from fissures during the Miocene period. Successive flows accumulated to great depths. Evidence indicates considerable time may have elapsed between some flows, for separating soil layers at certain locations contain plant and animal remains. When the voluminous oozings of the molten rock ceased, the Columbia River began entrenching itself in the then-horizontal plateau. As the river cut its channel, the Saddle Mountains were uplifted slowly enough for the Columbia to maintain its course.[1] It is possible that before the extensive lava flows came forth the river flowed more directly to present Pasco. Nonetheless, the lavas pushed the river bed northward and westward as successive layers covered the land. The increasing depths of lava may also have contributed to subsidence in the vicinity of Pasco, evidenced by a drop of approximately 25 feet per mile from the margins of the plateau.[2] In the Pliocene the Cascades began uplifting, and the creation of the arid Columbia Intermontane Province commenced.

Pleistocene glaciers, the first perhaps one million years ago, sent tongues of ice to the edge of the region, causing blockage of the Columbia and forcing its water to rise

Topographic Diagram, Adams County



W. R. Clevinger, Washington Crop and Livestock Reporting Service in *Adams County Agriculture,* County Agricultural Data Series, 1966.

along the margins and spread over the Plateau seeking new channels. The repeated retreat of glacial lobes gave meltwaters and the displaced river the occasion to erode temporary beds deeper and deeper. Approximately fifteen thousand years ago the last major episode of flooding crossed the plateau, leaving the Channeled Scablands as we now see them.[3]

Despite the fact that Symons[4] noted a parallelism of southeastern Washington streams to the Snake River, the major waterway of Adams County is perpendicular to it and to the Palouse River into which it empties before the latter turns south and joins the Snake. This is Cow Creek, known to the Indians as the more euphonious Cheranna. The river extends from the northeast section of the county some 25 miles southward. Three other streams are prominent in the county: Rock Creek, McElroy Creek, and Crab Creek. The last, divided into two parts, heads near Reardan and travels 175 miles southwest to its junction with the Columbia at Beverly, Washington. Lower Crab Creek, in the western portion of the county, rises in Moses Lake, whose principal source is spring-fed Rocky Ford Creek. The springs rise a few miles south of where Upper Crab Creek disappears into the stream's gravel bed, and it is assumed that part of the spring flowage is supplied by Upper Crab Creek.[5] Crab Creek's drainage area of 5040 square miles contributes little discharge to the Columbia. However, it is the only stream of consequence from the east, between the Spokane and the Snake, to add its waters to the larger river.

Lakes are not numerous in Adams County, but those of some note are: Cow, Sprague (Colville), Palm, Little Swamp, Big Swamp, Finnell, McElroy, Horseshoe, Crane, and Deadman. Many small bodies of water, often no larger than ponds, are unnamed. Springs occur occasionally, and several miles west of Othello a natural ice cave was discovered.

Although much of the county is fairly level to moderately sloping land, there are steep to hilly uplands and flats. Several coulees traverse the area, trending in a northeast-southwest direction. Eastern portions of the county have almost level outwash terraces and plains with rolling loessial hills. Loessial uplands of the center portion range from fairly level to steep, hilly topography. Major drainageways in the western part exhibit nearly level bottomlands and bisect gently sloping outwash terraces. Prow-shaped islands of loessial soil, remnants of ice-age flooding, exist between coulee channels. In the west of the county, tips of two east-west ridges, the Frenchman Hills and the Saddle Mountains, extend into the Central Plains section which forms the greatest part of the county. One topographic form seems to grade into the other without abrupt change.

Climate

Due to the Cascade Range, which modifies westerly moisture-bearing winds from the Pacific Ocean, eastern Washington exhibits climatic characteristics which are more transitional than marine. The Rocky Mountain chain further protects the region from extremes of weather produced by storms crossing southern Canada. Winters are the season of greatest precipitation with more than two-thirds the annual amount coming between October and March. From the beginning of September to the last of February snow is most frequent. Summers in Adams County are dry, hot, and sunny; inhabitants receive 85 per cent of the possible sunshine in July and August.[6]

The dominant climatic characteristic is the small amount of precipitation which in the county is related to elevation. Othello, in the western panhandle at an elevation

of 1100 feet, has averaged 8.16 inches of annual precipitation during the record keeping period, 1941-1960. Lind Experiment Station, situated in the center of the county (elevation 1625 feet), averaged 10.11 inches in a 29-year period. Ritzville, in the central northeast section at 1825 feet, has averaged 11.87 inches annually. Sprague, just into Lincoln County, has an elevation of 1925 feet and averaged 14.70 inches.[7] Relative humidity varies considerably from season to season and fluctuates most noticeably during a 24-hour period in summer when a range of 40 per cent is not unusual.

Increasing dominance of continentality is reflected by the wider range of annual temperatures. The county's lowest extreme, -30° F, was recorded at Hatton; the highest, 111° F, at the Lind Experiment Station. Othello registered the highest average maximums, 63.3° F; the lowest minimums, 36.8° F, were marked at Ritzville.[8] Summer afternoon temperatures often reach 95° F, whereas winter night recordings fall to readings between 15° F and 25° F. Cold snaps are not infrequent, and cold spells of any duration are an exception. One settler, John E. Smith, who lived some eight miles above the falls of the Palouse River, recalled that in 1878 or 1879 he saw Palouse Falls entirely frozen.[9]

The growing season is longest in the county's southwest where, near Othello, the frost-free season averages between 160 and 200 days with May 1 the average day of the last freeze. The first 32° day in autumn usually comes after October 1, giving an average 150-day growing season to the remainder of the county. Higher elevations in the eastern part of the county, where air drainage is poor and killing frosts come earlier, experience a shorter growing period.

Adams County and eastern Washington exhibit at least two weather phenomena which merit comment. Dust storms usually occur in spring and fall when rapidly moving weather systems come to the region and pick up varying amounts of soil. "Extreme wind speed at thirty feet above the ground can be expected to reach or exceed 50 m.p.h. once in two years."[10] The second weather phenomenon is the chinook wind of winter months which brings a rapid rise in temperature. Results can be devastating. If there is snow and the ground is frozen, most of the melting is lost as run-off. In cultivated areas, if the ground is thawed, erosion can be severe.

Soils

Of prime importance to the geographic and historic development of Adams County is soil. Six soil associations (landscapes that have a distinctive proportional pattern of soils) exist, two each in locations where precipitation is moderate, moderately low, and low. The soils, formed from wind-deposited and alluvium-wind-deposited materials, rest on rock foreign to their genesis.

In the eastern portion of the county where precipitation averages 12-14″, soils have a dark-colored surface layer and are formed in silty materials under bunchgrass. These are usually well drained with lime at about four feet. Although wind erosion is a problem in this area, water erosion is even more serious. Precipitation is moderately low (9-12″) in the central portion where soils are well drained and also formed in silty materials under bunchgrass. The surface layer is only slightly dark colored; lime is found at three feet, except where bedrock or hardpan is near the surface. Wind and water erosion problems escalate from slight to severe; moisture conservation is an acute problem. In the western portion of the county where precipitation is low (7-9″), well-drained soils formed under rather sparse bunchgrass have a light-colored surface layer. Lime is encountered at approximately two feet. Major difficulties are moisture

conservation and wind and water erosion. Portions of this section are under development for irrigation by the Columbia Basin Irrigation Project.

Early settlers recognized few of these differentiations. Some saw a degree of potential soil fertility in what was considered a barren wasteland, suitable, at best, only for grazing. In eastern Washington several years before the turn of the century reports came from longer-settled locations of successive crops grown on the same piece of land with neither fertilizer nor rest, and with always excellent results.[11] It took many years for the new settlers gradually to learn the ways of nature in the new land they were settling. An early surveyor of Adams County, A. L. Coffee, later admitted he initially saw no value in the soil of the county. By 1894, however, he became aware of similarities between soil in the vicinity of Mt. Vesuvius and Adams County, noting that the former improved under proper farming practices rather than deteriorated. He became convinced that the soil of Adams County was of the same character.[12]

Ecological Changes

Various climatic changes during geologic time produced substantial alterations of plant and animal communities. Even recently, since the early explorers, certain plant and animal species in eastern Washington have undergone grave changes. David Douglas, the renowned botanist, visited the region in 1826, making pertinent observations. Numerous muskrat and beaver lived along tree-lined streams; racoons, weasels, mink, and the skunk were frequently encountered. Rabbits, sand hill cranes, curlews, coyotes, and blue and ruffed grouse were noted. Hunters for subsequent exploring parties often bagged deer and antelope for the evening meal. Even cougar and bobcat were, at least casually, far onto the prairie in southeastern Washington.[13] Native blue bunch wheatgrass, Idaho fescue, and sandberg blue grass are now less abundant. Tarweed, sagebrush, fireweed, and cocklebur have expanded their range. Extensive grazing in the latter decades of the 19th century changed the plant composition in many localities, causing unique plant communities to be established.[14]

In historic times conspicuous changes have occurred in the bird population. No longer do we have significant numbers of the California condor, trumpeter swan, or whooping crane, although extreme care by game biologists has nurtured the almost-extinct species. Greatly reduced in number are the blue heron, long eared owl, and whistling swan.[15] In Adams County especially, cultivation brought a catastrophic reduction of sharp-tailed grouse and sage hens. To counter balance their disappearance, Chukar partridge, ring-necked pheasant, and Hungarian partridge were introduced and successfully established themselves. Extensive grain fields and water in pot holes and coulee basins of the vicinity have made the area attractive to a variety of waterfowl.

Domestic animals, introduced by man, triggered far-reaching responses. Eastern Washington was truly a horse heaven in the 18th and 19th centuries for Indian ponies which fed upon the nutritious native grasses. After 1850 ranchers entered the region, "bringing with them concepts of grazing from the more humid lands of the Midwest, little realizing the delicate adjustment between vegetation and grazing animals where rainfall does not exceed 10-15 inches."[16] Extensive and intensive grazing ultimately changed plant communities which, in turn, vitally affected wildlife populations. Cattle also influenced small mammal species as overgrazing saw the increase of ground squirrels and other small rodents and lagmorphs. Wolves, cougar, coyotes, bobcats, and occasionally even bears which preyed upon these, and sometimes upon the cattle as well,

were attracted to the area, thus altering to a considerable extent the biotic community. Replacement of native prairie by croplands also had a profound effect on the ecology.

Wire fences acted as deterrents to wind velocity, resulting in dust deposition in summer and snow deposition in winter. Shrubs (mostly rose and snowberry) responded to these soil and moisture conditions and established themselves. Thickets thus developed accentuated wind retardation. . . . Nonetheless though farming operations in the pioneer period (1875-1910) were restrictive, they were not sufficient to cause extirpation but rather a gigantic shuffle of habitats.[17]

Land Use Capability Classes in Adams County, Washington

Very good land with deep, nearly level soil having few limitations.

Good land with minor limitations such as gentle slopes, moderately shallow soil, or slight erosion hazard.

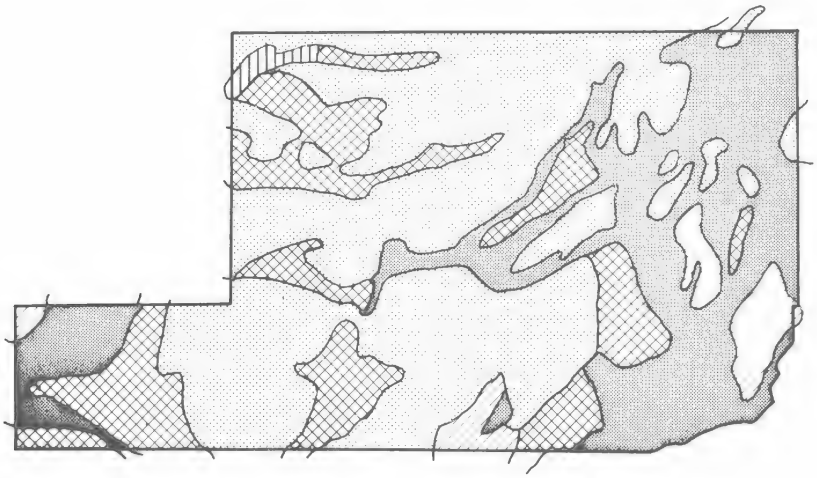
Moderately good land with major limitations such as steep slopes, shallow soil, or severe erosion hazard.

Fairly good land, suitable for occasional cultivation. Severe limitations require careful management.

Very well suited for grazing but unsuited for cultivation.

Well suited for grazing with minor limitations such as moderately steep slopes or shallow soils.

Fairly well suited for grazing, with major limitations such as steep slopes or shallow or droughty soils.



SOURCE: U.S. Soil Conservation Service Map: Washington, Generalized Classification of Land According to its Capability for Use, 1949.

Adams County Agriculture, County Agricultural Data Series, 1966.

Man

Native Peoples

Recent discoveries by Washington State University scientists indicate man's presence in eastern Washington over 11,000 years ago. Finds at the Lind Coulee archaeological site, dating from the Anathermal period (9000-7000 years before present), indicate that early man was primarily a hunter. Bison, the main food source, was supplemented by small game animals and waterfowl. Use of vegetable products was slight. Stallard speculates that climatic changes in the Altithermal (7000-4000 B.P.) may have triggered an increasing dependence on fish as certain animal species retreated from the region.[18] Xerophytic plant communities appeared, and certain plants may have been added to man's diet of small game animals.

Data from other sites in eastern Washington tell us that at least

> . . . throughout 6000 years of cultural history there is no evidence of an abrupt . . . cultural change, or of a drastic change in economic patterns . . . . Cultural history of this region was characterized by great stability . . . . Change took place gradually, principally by the accretion of new elements and by stylistic change.[19]

Thus, for thousands of years native peoples apparently lived in the same general manner. They used the land mainly as a stalking ground for the game upon which they subsisted, and also for brush and wood for shelter and fuel, and perhaps occasionally they gathered some vegetal material.

Coronado's outposts in the southwestern United States were the source of horses which through trading and theft ultimately found their way to the Columbia Plateau. By the time of Lewis and Clark, native populations had become accustomed to this new mobility. Alterations in life were intensified by the horse. Because further food sources could be reached, more people were able to live together in a village. Leisure time resulted and concomitant with it, cultural development.

The rich bunchgrass of Adams County provided food in enormous quantities for the Indians' horses, a measure of tribal wealth. But this area primarily served as a thoroughfare for various tribes who, from the Snake River, followed trails paralleling the courses of principal creeks and wore a pathway through the desolate countryside.

The future Adams County offered few inducements for permanent villages compared with the forested rim of the Plateau. Mountain valleys were alive with a profusion of game, roots, and berries, mainstays of the Indian diet. Streams and lakes offered fish in abundance. There much of the regional Indian population lived. An exception was the small and primitive Palus tribe, considered comparatively new arrivals.[20] Salishan tribes occupied most of the area south of the main Palouse River and the banks of the Snake until encountering the Nez Perce tribe, a Sahaptin people. In winter, family groups found snug sites in deep canyons along the sides of the Snake. Seasonal runs of salmon temporarily brought great numbers of people speaking different dialects to fishing stations along the Snake and its tributaries. The falls of the Palouse River was one such site. Duck eggs were gathered in the potholes, roots dug in selected areas of partial moisture, some berries picked as they ripened in the summer sun, fish and game taken. Even an area burned to drive the game usually re-established itself luxuriantly the following year with no effort on the part of the regional inhabitants.

The Northwest's first publicist, John Ledyard, was unsuccessful in his attempts to maintain the interest of officials and businessmen in the region. Proferred support evaporated several times. Thomas Jefferson caught a snatch of Ledyard's dreams but hesitated until Alexander Mackenzie's publication, *Voyages,* assisted in solidifying the President's designs. Plans for a western excursion had been postponed more than once previous to the famed Lewis-Clark Expedition.

In 1806 Lewis and Clark returned with categorized knowledge of the Northwest; soon after fur trading forts were built on the Plateau. The first was Spokan House, built at the confluence of the Spokan and Little Spokan rivers in 1810. In September the following year Fort Okanogan was erected at the Columbia and Okanogan by the Astorians. Supplies for the inland posts initially came from Astoria. Ladened canoes, rather than fight the unpredictable Columbia, followed the Snake River to its junction with the Palouse. Here, at an old Indian crossing, the canoes were emptied. Securing horses from the vast herds of nearby tribes, the fur traders loaded the goods destined for the interior posts and proceeded overland. Some followed an old Indian trail west of the Palouse River canyon and along Cow Creek through future Adams County to Spokan House. Others, from the Snake River crossing, veered westward toward present Othello, skirted Moses Lake and later the depths of the Grand Coulee, before reaching Fort Okanogan. Ross Cox, a fur trader, separated from companions as he journeyed northward from the Snake toward Spokan House, wandered aimlessly for two weeks across some parts of Adams County before finally encountering a solitary Indian family who ministered to him, saving his life.

Posts of the vigorous North West Company dotted the Rocky Mountains and the adjacent regions while the Hudson's Bay Company concentrated its efforts in the East. By 1821 bitter competition between the North West Company and the Hudson's Bay Company had reached its peak, and the Crown forced consolidation of the two rivals. Reorganization brought with it dictates for at least partial self-sufficiency at the fur posts. Least profitable of the establishments was Spokan House, which was replaced in 1825-26 by Fort Colvile, located near the Kettle Falls of the Columbia. After 1826 the Indian pathway to that point which paralleled Cow Creek through Adams County-to-be saw increased traffic. Gardens for the subsistence of fur trade employees changed the land little. Essentially, the fur trade took from the land, causing only minor changes in the ecology. It was the retired employee, planting crops by which he existed, who began the alteration of the land. Yields of potatoes and wheat grown in the Colville Valley influenced the Spokane tribe, some of whom grew wheat in the Valley, possibly as early as 1835.[21]

Once missionaries arrived, they encouraged agricultural practices among the native inhabitants. Although having little previous experience with farming, one of the earliest Americans in the area, the Reverend Elkanah Walker, stationed at the Tschimikain Mission near present Ford, Washington, did not anticipate much future regional development. He stated:

> I think I am safe in saying that there are thousands of acres where a man by ordinary cultivation could not raise enough to support himself & if he could he could not find wood or water sufficient to cook it. There are places between here (Tschimikain) and Walla Walla of thirty or 40 miles distance where there is neither wood nor water to be found. Even if there were a good supply of wood the want of water & means of irrigation would render it wholly unfit for cultivation & even for grazing.[22]

In the early 1840's settlers began to accompany the missionaries across the continent

to the Pacific Slope. Most scorned eastern Washington as a desertlike, grainless region. For years Americans had received geographical reports of their expanding nation from those who had been there or from those who had heard from others who had been there. Competence for assessment was rarely questioned. Still greater credence was given to journals and publications of explorers and army reconnaissances. The 1806 explorations of Pike and the apparent substantiation by the Long Expedition of 1819-20 had led to rumors of the existence of the Great American Desert in the midsection of the country. Similarities in landscape brought the appellation to interior Washington.

Isaac Stevens' perceptive mind and West Point training permitted a keen assessment of eastern Washington's potentialities. ". . . here I was astonished not simply at the luxuriance of the grass but the richness of the soil. . . . The country is a rolling tableland and the soil like that of the prairie of Illinois."[23] In 1856 Stevens attempted to counteract negative attitudes about the region when he spoke to the annual Legislative Assembly saying

> We . . . find that cultivation may be commenced some days earlier in the Territory than in places several degrees south in the Atlantic States, and some weeks earlier than in places of the same latitude. Allowing for the close vicinity of all the western posts to mountain ranges, we may suppose that a still greater difference exists in certain localities on the Great Plain* where the greater dryness of summer also requires an earlier cultivation for success . . . . Grazing is excellent throughout, precluding the necessity of laying up much supply of fodder.
>
> Even comparing the elevated interior with various places further south we find the advantage in our favor which will not be excepted in any part of the interior of Oregon, except near the Columbia, on account of the greater elevation of all parts of that country.
>
> . . . there seems no climatic reason why the interior of Washington Territory should not produce abundantly . . . .[24]
>
> * The Columbia Plateau was called the Great Plain or the Great Plain of the Columbia in this period and is not to be confused with the Great Plains east of the Rocky Mountains.

Nonetheless, pioneers from the East sought a familiar green landscape, a requirement met by lands west of the Cascades. Wagon trains headed for California or the Oregon Country—the part west of the Cascades and Sierras—that looked somewhat like home.

Land Acquisition

The settlers acquired land in a number of ways. The Oregon Donation Land Law of 1850 established the pattern of family farms on the western side of the Cascades. Most were large and somewhat dispersed, for a married couple was granted a square mile of land. Few Donation claims were taken in eastern Washington (then part of Oregon Territory). Although the law stimulated agricultural settlement, Isaac Stevens pointed out to the Legislative Assembly in 1856

> Congress . . . passed a donation law, inviting settlers to locate claims, first west and then east of the Cascade Mountains, and public surveys had been ordered to be made over this domain. But the Indian title had not been extinguished. This was a bitter cause of complaint on the part of the Indians . . . . had I known when the council at Walla Walla was convened, what I learned afterwards, I should not have convened that council.[25]

In eastern Washington the discovery of gold in northeastern parts of the Territory and violation of treaties generated bitterness, violence, and finally an Indian war. Conditions became so severe that the region was closed to settlement.

Westward movement was further encouraged by the Homestead Act of 1862 which, after five years' residency and minimal "improvements," gave free title to 160 acres. These smaller segments did little to stimulate settlement east of the Cascades for in an arid environment they were insufficient for profitable stock raising or cropping.

However, by planting 10 acres to timber, an additional 160 acres could be acquired under the Timber Culture Act.

A third means to possess land was through purchase of parcels granted to the railroad. Five- and 10-year contracts, priced from $2.60 to $6.00 per acre, were available for agricultural lands. Credit buying required residence and crop production. In the central plains of the Territory and the Palouse full sections were commonly sold or leased on a long-term basis.

Pre-emption was a common means of acquiring clear title to land. Any citizen, or anyone intending to become a citizen, who was head of a family or single and over 21 years of age, could obtain 160 acres after residing on the property for six months and paying $1.25 per acre.

Governor Squire reported that for the fiscal year ending June 30, 1885, land transactions in the Walla Walla District Land Office, which included Adams County, involved 185,192 acres.[26]

Settlers—Stockmen

Mining advances generated settlement in the Walla Walla Valley early in the decade of the 1860's. When the best lands in the Valley were occupied, settlers moved north of the Snake River to secure pasture for their livestock. The bunchgrass hills were deemed worthless for crops. First settlers were cattlemen, often former gold miners or government freighters who were persuaded to remain in the region because of the market created by the mining rush. Natural conditions which made Adams County attractive as pasture for herds of Indian ponies also made it ideal rangeland for cattle.

Original settlement in Adams County-to-be was along Cow Creek, but "few came with a view of establishing a home there, their purpose being to graze stock for a few years and then abandon the country, raising some grain in the meantime for their own use, and possibly a little to sell, for anybody who wished to buy."[27] Lured by dreams of quick riches, moderate climate, and ready forage, ranchers and would-be ranchers made their way to eastern Washington. Too many came—and by then, there were already too many cattle. Mining markets in the Territory and western Canada virtually disappeared by 1869, and stockmen sensed disaster. Local consumption made few dents in herd surpluses.

> A slump in the cattle trade hit the Pacific Northwest from the close of 1872 to the spring of 1881. . . . The boom days were over and cattlemen faced difficult times . . . .
>
> Cattlemen began to devise means to dispose of the surplus stock. John West and Company began canning beef, using the salmon canneries on the lower Columbia . . . . The experiment was not a financial success.[28]

Several months following Custer's defeat in 1876 and subsequent harassment of the Indians by United States troops, treaties with the Sioux and Cheyenne were signed, permitting grazing areas to become available in eastern Wyoming and Montana. Rollison maintains that this development created a boom for cattlemen in the Northwest because stockmen on the Great Plains had misrepresented their herds in stock prospectuses and feared legal action.[29] Thus they needed cattle in a hurry. Inland Empire beef answered their needs; they were able to withstand the climatic variability better than Midwestern beef, and were considered superior to Texas cattle. Additionally, they had no tick fever, a current problem.

Cattle began to move eastward in the early 1880's across the Rocky Mountains over two routes: one going through southern Idaho via Boise City and the second following the Mullan Road. Herds driven to eastern ranges numbered thousands of beef. Over 10,000 eastern Washington cattle were driven to Montana in 1880, and the Inland

Empire contributed significantly to these markets for the next several years. Although 1885 was especially prosperous, within two years such shipments were drastically reduced and virtually ceased by 1890. Shipment by rail to distant slaughter houses signaled the passing of trail drives.

During these years extension of croplands to former range areas and the multiplication of horses on the range competed for pasturage. Eastern portions of Adams County were settled in the 1880's, but it was 1901-02 before western areas developed. George Bassett estimated in 1878 that the entire white population of what became Adams County was 15 persons.[30] In 1886 Ritzville boasted a population of approximately 150; the county had 350 additional residents. Many towns in the county were initiated by the railroads and augmented by the arrival of immigrants who settled in town or on farmland nearby.

Sheep raising made inroads into formerly exclusive cattle country in 1879. Sheep herding had long been favored as a frontier enterprise, offering opportunities to men of small means, and utilizing inferior range. Besides the advantage of low marketing costs and the comparative nonperishability of wool, sheep were able to adapt to a variety of conditions and to do well on weedy, shrub-like types of vegetation. Initially only a few ranchers raised sheep, but soon it was not uncommon to see bands of 2000-5000 animals passing through struggling villages on their way to summer forage. A prominent route was through Umatilla and across the Snake to Crab Creek, then around Big Lake (Colville Lake), Wilson Creek, and Four Lakes. (See Tables 1-3 for livestock in Adams County in this period.)

TABLE 1. Livestock.*

Year	Cattle	Milch cows
1890	5,132	754
1896	8,205	——
1900	8,766	——
1903	10,041	——
1907	6,440	2,150
1910	8,829	——
1920	4,981	3,912
1930	6,435	1,895
1935	12,662	——
1940	9,161	——
1950	19,879	885
1954	23,447	441
1959	29,466	195
1964	47,823	132

* Censuses of the United States and the State of Washington, pertaining to agriculture, 1890 through 1964.

TABLE 2. Livestock.*

Year	Horses	Mules and asses
1890	4,443	25
1900	10,879	128
1903	12,415	——
1907	13,077	758
1910	16,603	1,726
1920	15,939	2,239
1930	8,849	2,705
1935	6,542	2,170
1940	2,193	205
1950	720	(includes mules and asses)
1954	437	(includes mules)
1959	490	

* Censuses of the United States and the State of Washington, pertaining to agriculture, 1890 through 1964.

TABLE 3. Livestock.*

Year	Swine	Sheep
1890	634	8,890
1896	1,814	15,700
1900	2,844	7,275
1903	4,453	28,736
1907	3,652	18,261 (includes goats)
1910	6,200	20,832
1920	5,690	18,405
1930	2,515	45,723
1935	2,355	39,135
1940	1,383	36,188
1950	1,343	6,940
1954	1,506	6,970
1959	6,509	5,082
1964	4,446	3,085

* Censuses of the United States and the State of Washington pertaining to agriculture, 1890 through 1964.

Ranching Problems

After 1880 the railroads began attracting scores of pioneers to the Inland Empire. Newcomers fenced springs and waterholes, developed homesteads, and pushed rangelands to less desirable locations. Stock, wandering through maturing crops, were sometimes shot to protect the yields. Soon the settlers began agitating for herd laws, an ominous sign for the cattleman. Stockmen lamented that free range had almost disappeared and banded together to resist the invasion of farmers, but without notable success. Many correctly perceived things to come, sold most of their cattle, and became grain farmers. The increasing number of farmers kept a small herd of cattle which they fattened on the grain left in the fields after harvest.

According to the *Adams County Record,* James G. Bennett was the first person to farm in the county. In 1879 he planted approximately one hundred acres to wheat—which ground squirrels ate with obvious relish. The next year he tried again on his homestead north of Ritzville and had better success. Philip Ritz located in the northern part of the county in 1878. Five years later he was advertising in many of the regional newspapers, offering for sale a variety of trees grown at his Ritzville nursery.

Settlers in great numbers began making inroads into cattle country in 1883. The previous fall this section, which included Adams County, was considered to be of little value agriculturally.[31] The year official political status began for the county, 1883, a group of German-Russian families arrived and took lands west of the original Ritzville settlers. Many subsequent immigrants came from near Canton, North Dakota. Their success in Adams County brought additional friends and relatives to the new county. (See Tables 4 and 5.) Also in 1883, one of the largest ranches in Washington began, most of which was situated in Adams County. This was the Harder ranch. Jacob Harder, then an immigrant of nineteen, began buying horses from Indian Wolf, a Palous chief. Through the years he increased the family holdings, reaching a peak in 1937 of 120,000 acres, divided between wheat and cattle.

Cattlemen recognized the grazing potential of eastern Washington. Initially, things went well, but then severe livestock losses began. Few losses in Adams County were caused by poisonous snakes and plants, rustlers, heat, and lack of water. Through the decades, however, stockmen lost thousands of animals due to snow and bitter cold and their lack of preparation for extreme conditions. Widely read and accepted testimonials, such as the following, unwittingly deluded many. In discussing the snow and his search for a pass through the mountains, John Mullan wrote

TABLE 4. Number and size of farms (acres).*

Year	3-9	10-19	20-49	50-99	100-499	500-999	1000-1999	over 2000
1890	—	—	2	3	343	35	16	—
1900	—	1	3	6	485	171	112	—
1910	4	5	10	21	563	383	277	—
1920	4	2	8	17	364	419	268	—
1930	10	4	8	7	180	285	320	—
1940	6	—	5	3	107	228	301	—
1950	6	7 (10-29 acres)	1 (30-49 acres)	3	60	171	350	—
1954	1	3 (10-29 acres)	4 (30-49 acres)	39	98	158	334	—
1959	13	12 (10-49 acres)		43	232	148	195	—
1964	13	11 (10-49 acres)		32	216	134	186	152

* Censuses of the State of Washington pertaining to population, 1890 through 1964.
Censuses of the State of Washington pertaining to agriculture, 1890 through 1964.

TABLE 5. Population.*

Year	Total	Rural farm	Rural nonfarm	Urban	Density
1885	500 (estimated)				
1890	2,098				1.11
1893	2,185				1.15
1896	3,500				1.9
1900	4,840				2.03
1910	10,920				5.77
1920	9,623				5.08
1930	7,719	4,058	3,661		4.07
1940	6,209	2,818	3,391		3.27
1950	6,584	2,327	4,257		3.48
1955	9,200				4.86
1960	9,929	2,805	4,455	2,669	5.24
1967	11,538				6.09
1968	11,791				6.23

* Censuses of the State of Washington pertaining to population, 1890 through 1968.

We can avoid this depth of snow . . . by going farther north. Paradoxical as it may appear to some, it is nevertheless true, that within reasonable limits in latitude 47 and 49 we find this phenomenon to hold, that the farther we go north the more mild the climate becomes, less severe the cold, less deep the snow. This is shown particularly via the Clark's Fork of the Columbia, where one can travel during the most inclement weather . . . .

The Indians who inhabit these mountains cross and re-cross the range . . . in winter. Their horses are of a peculiar hardy nature that withstand the phases of winter, subsist solely on the native grasses found along the hillsides in winter and in the valley in summer. I have often compared the perfectly careless abandon of these people, so far as their stock is concerned . . . with the sedulous care that the farmers of New England and in the Northwest States evince in procuring and husbanding forage for their stock, during the dreary six months of winter. It is this important fact of mild and genial winter, with rich and nutritious grasses, that render this region one of the finest grazing sections to be found in the world.[32]

Twenty years later, in 1885, the *Adams County Record* of November 3 carried a *Chicago Daily News* release which quoted Colonel Frank Parker, editor and proprietor of the *Daily and Weekly Statesman* (Walla Walla, Washington Territory), in referring to the region of the Inland Empire as follows:

. . . In the eastern division the land is fine rolling prairie and generally is well watered. It is a great country for stock of all kinds, which live there the year around and are put in fine condition without any food except that which is provided by nature. . . .

Many lost their entire herd because of ignorance of preparation for winter. The winter of 1846-47 was especially severe. In 1861-62 thermometers registered –40° F. and crushed the ranching operations of many whose future appeared assured in the

autumn of 1861. A savage March snowstorm finished off reeling survivors of the earlier bitter cold. Starving cattle drifted to the rivers, fell into deep holes, and died, too weak to attempt their own rescue. Thousands of dead cattle lay along the rivers of eastern Washington. Spring brought an unbelievable stench.

Losses during the winter of 1880-81 often exceeded 50 per cent. These were especially disastrous for they left the industry weak and uncertain at the time farmers were vigorously commencing to crop the land. As the following decade started, the tragedy was again repeated.

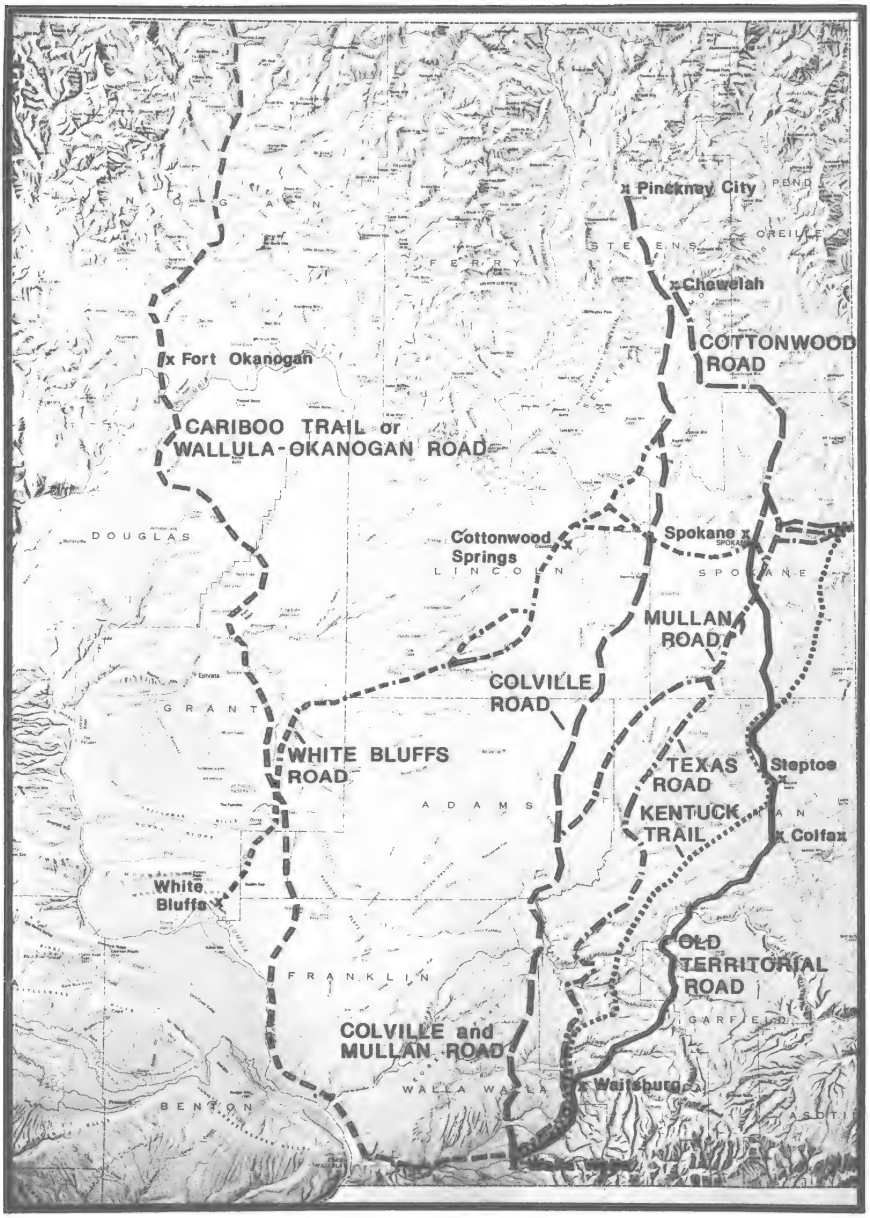
Early Routes in the County

Supplies in the early days came from Walla Walla, then the largest town in the Territory east of the Cascades. Usually two trips a year were sufficient to bring needed supplies back to the ranch.

There were no roads at first and pioneers followed Indian paths through sagebrush and bunchgrass. The first important route of the pioneers connected the army post at Fort Colville with Fort Walla Walla, then the only settlement in eastern Washington south of the Spokane River. Major Lougenbeel and four companies of the 9th Infantry pioneered the route, following the old Indian trail from Walla Walla in June, 1859, and crossing the Snake below Texas Ferry. Natural obstructions along the way were by-passed while still following the easiest and most direct route which afforded sufficient grass and water for draft animals. The Colville Road, as it was called, paralleled Cow Creek valley after leaving the western side of the tableland along the barren and rugged Palouse River canyon. It skirted the east side of Big Lake (Colville or Sprague Lake) and continued past present Sprague to Rock Creek and Willow Springs. Passing four miles to the west of Medical Lake, the Colville-Walla Walla route crossed Deep Creek, coming upon Coulee Creek at its forks. From there it was a short distance to the "winding ford" of the Spokane, upstream a short way from the present Washington Water Power dam. The road blazed by Lt. John Mullan was coincident to the Colville Road until the vicinity of present Benge where the Mullan Trail crossed Cow Creek and veered easterly, passing some twelve miles southeast of Cheney. In the early 1860's wagons could cover the 624 miles from Ft. Walla Walla to Fort Benton on the Missouri River in seven or eight weeks. Pack trains to the same destination took five weeks.

Weary travelers along this road were able to refresh at Henry Wind's, who with A. B. Bernecke in 1864 established a squatter's claim on Cow Creek. The property then passed to Favre or Saber, a Frenchman, in December, 1868, and subsequently to George Lucas in August of the following summer. The Lucas homestead continued, as had its predecessors, as a way station for travelers. It was situated about a day's journey north of the Lyons Ferry crossing of the Snake River. Near there, a later route, called the "Cottonwood Road," divided from the Colville-Walla Walla route and went up Cow Creek valley. It passed the J. F. Coss homestead in 1872, a principal stopping place, and passed the Sinks east of Ritzville, north to Harrington, Lord's Springs, and Cottonwood Springs. From that place it angled northeastward to the "winding ford" of the Spokane.

Late in the fall, 1865, Bill Wilson built a cabin at the head of Big Lake (Colville-Sprague Lake today), another stopping place enroute. Tom Reynolds owned the establishment later.[33] The Mullan Trail was three miles from the Bassett homestead when the latter was constructed, but the road soon swung by the house which became one of the most popular lodging places in eastern Washington.



Redrawn from Freeman, O. W. "Early Wagon Roads in the Inland Empire." *Pacific Northwest Quarterly,* Vol. 45, No. 4, October, 1954.

When miners streamed across the Inland Empire in the latter 1850's, many were channeled through Walla Walla and Lewiston, to which point steamboats ran by 1861. Others disembarked from Oregon Steam Navigation Company's boats at White Bluffs Landing to where service was extended in 1863. The boat operated between there and Wallula until winter closed navigation on the river. Soon a primitive roadway was made from the Columbia along Crab Creek, skirting the foot of Moses Lake and passing a few miles south of Odessa. Following the creek again, the White Bluffs Road, as it became known, traversed the ridge between Duck Creek and Lake Creek and then went through present Davenport, Mondovi, Deep Creek, and Spokan Falls. From there it continued to Westwood and subsequently to the Steamboat Landing on Pend Oreille Lake.[34] After 1867 traffic over this route declined as ships made their way up the Missouri to Fort Benton, the jumping-off place for the Blackfoot diggings, then the Eldorado. A new gold rush and military movements over the road from White Bluffs revived its use in the 1880's.

Settlement

Prior to the impetus of mining discoveries in northeastern Washington Territory, the region between the Columbia and the Rockies offered little inducement to settlement. Fairly accurate reports of potentialities went unheeded, and the notion that limited agricultural land existed was prevalent. The region's relative isolation from the main stream of continental immigrant routes resulted in few side excursions to evaluate the land, for westering pioneers at that point in their journey were exceptionally weary. They were seeking a place that resembled the land they left; the landscape between the Rockies and the Cascades did not fit that description. Eastern Washington counted less than 100 families in 1850, most of which were associated with the floundering fur trade. Mining discoveries in the ensuing decade stimulated interest in the region, and miners, as well as the parasite population which follows, came in large numbers. Soon, however, the mines gave out, and evidence of overgrazing was prevalent. Subsequent decades saw the necessity of limiting the numbers of stock so that there would be natural feed the next years.

Seeking additional markets for their produce, stockmen and farmers shipped flour, the one manufactured product of the region, downriver to Portland in 1868 via the facilities of the Oregon Steam Navigation Company, which then monopolized regional transportation. Although a stage line ran the 25 miles between Walla Walla and Wallula on the Columbia, valley residents clamored for a railroad by which they hoped to reduce some of the exorbitant shipping costs. Freight charges on the overland route varied from $5 to $13 per ton, and freighters were sometimes charged additionally for waiting to unload at the Wallula Landing. Although a railroad charter was granted in 1862, construction did not begin until 1871. Its immediate effect was to reduce costs of transport from Walla Walla to Wallula. However, wheat transportation from Dayton or Waitsburg to Portland in 1880 involved 10 to 14 handlings with proportionate costs.[35]

Inducements for the Farmer

By 1875 advertisement of the Territory to prospective settlers was well underway. Lecture-circuit speakers toured eastern cities extolling the advantages of the Northwest. Newspapers and magazines painted rosy, occasionally inaccurate pictures. Governor Elisha Ferry told the 5th Biennial Session of the Legislature of an association of Wash-

ington women who collected statistics, answered letters, and conveyed to those inquiring about Washington Territory various facts regarding the climate, agriculture, manufacturing, and commercial facilities.[36] Several towns had immigration societies which urged settlement in this or that community. Around 1875 W. H. Newell of Walla Walla published the booklet, *Homes in the Walla Walla Valley, with a Description of the Country, Its Resources, and Advantages.*[37]

North of the Snake River immigration received its first stimulus when the Northern Pacific Railroad began building in 1879. Special immigrant bureaus and agencies were set up throughout the United States and Europe. Speakers successfully appealed to various groups and nationalities. With the Palouse as a magnet, settlers flocked to the Territory. The Ritzville District was then beyond the edge of attractive land, but by 1883 the nucleus of the German-Russian settlement took lands there. Government land offices in Washington Territory entered nearly 8000 applications for public lands in their books in 1884,[38] but the scantily watered sections of western Adams County were avoided by most. (See Table 5 for county populations.)

Settlers found Adams County attractive partly owing to reports, measured by a committee, of one acreage yielding 800 bushels of wheat on 10 acres,[39] and to articles, such as *Profits from a Palouse Farm.* The writer of that article assured the reader the yield of 46 bushels to the acre was a good one but not large because of an estimated 20 per cent loss. He then continued

> To show that farming in the Palouse country pays the cost of purchase price, improvements, labor, taxes, etc. are given below, together with the receipts of 112 acres, the remaining seven (of Mr. George Speake's farm in the Palouse) being used for other purposes for which there is no cash return as yet.
>
> | | |
> |---|---|
> | Purchase price of 119 acres | $2,300.00 |
> | Fencing | 100.00 |
> | Breaking | 300.00 |
> | Seed | 60.00 |
> | Harrowing and rolling | 120.00 |
> | Heading | 140.00 |
> | Threshing | 250.00 |
> | Hauling grain to warehouse | 50.00 |
> | Taxes | 13.00 |
> | Total | $3,363.00 |
>
> Received from 112 acres—5,147 bushels of wheat @ 72½¢ for a total of $3,731, leaving a surplus of $368.57 after paying for the land and all other improvements, or a profit of $2,438.57 after charging 10% interest on the $2,300 investment.[40]

Much experimentation preceded the development and selection of suitable wheats for eastern Washington. G. H. Kanzler in 1885 sowed Australian Bluestem which yielded 45 bushels an acre on the second plowing. By the mid-twentieth century Bluestem had been replaced by superior varieties. The first genuine winter wheat in Adams County was Michigan Bronze, which gave poor yields and shattered badly. In 1896 early-day farmers secured a carload of Jones Winter Fife for seed. The Fife, Turkey Red, and Forty Fold became the standard varieties at the turn of the century. (See Table 6.)

Backgrounds of the Farmer

A large percentage of the incoming population was accustomed to a farming life in the Midwest. The mid-latitude forest lands from whence they came receive moderate amounts of precipitation, ranging from 20 to 40 inches annually, which is well distributed throughout the year. Maximum amounts come in spring and early summer, frequently as thunderstorms. Midwestern climate varies from the winter subarctic to

TABLE 6. Crops.*

Year	Wheat Acres	Bushels
1890	6,079	45,855
1900	88,025	1,203,670
1910	332,505	4,943,867
1920	308,821	3,910,240
1929	315,132	4,002,669
1934	259,692	3,867,848
1940	300,819	5,444,452
1949	374,216	7,993,584
1950	375,000	8,327,400
1954	292,508	7,366,827
1955	277,800	6,825,000
1959	253,497	8,558,346
1960	259,000	8,161,000
1963	269,200	9,009,600
1964	266,511	8,647,585

* Censuses of the State of Washington pertaining to agriculture, 1890 through 1964.

the hot humid weather commonly experienced in equatorial locations. Crops were usually planted in the less-productive soils developed under characteristic humid continental climates. Much of the western part of the Midwest is covered with loess. Great river valleys dominate the region where floods of centuries have deposited rich soil in the bottomlands, leaving uplands comparatively barren and of little agricultural value. In the western sections the natural vegetation was grass, often growing as high as eight feet. Near the 98th meridian the short grass country begins.

In eastern Washington newcomers sought and selected a replica of lands they had left east of the Rocky Mountains—timbered bottomlands with nearby water. Western yellow pine served as a beacon, and they homesteaded on the soils which supported this xerophytic tree. A number of families, spurred by the prospect of railroad building in the area, located on Union Flat Creek in the summer and fall of 1869. By 1870 there was a population of 118 in the Union Flat country where three years before there had been none.[41]

Transportation in the County

Population soon dispersed from original places of settlement, and before long roadways between newer sites and the older ones were a necessity. Local stage lines operated from various points throughout the region; one of the earliest was the Northwestern Stage Company which began operations in 1871. Its coaches brought light freight and passengers to steamboat landings along the Snake River. Shortly after the establishment of Ritzville in 1880, Lt. Symons surveyed a wagon road from there to Camp Chelan, a distance of 107 miles, which helped to stimulate development in the area it served. The Ritzville Road connected that town with Washtucna, and the road leading to Lyons Ferry was used by the entire region, bringing the traveler eventually to Walla Walla. This same road extended northward to Wilson Creek, from which a route of sorts wound through the countryside to Chelan.

Pleas from Badger Mountain folk were taken up by the *Adams County Record* in 1885. The 150-mile distance to Spokan Falls was a wearisome trip to acquire their needed supplies. A road from their area to Ritzville would have shortened the mileage

by 53 miles and, of course, would have helped Ritzville establish itself more firmly as a trading center. To encourage this endeavor, the newspaper noted that there was already a road located "from Ritzville in that direction to the northwest line of Adams County." Petitioners the year before, 1884, had asked for a road across the county, running from where the old Neppel Road (Rosenoff) touched the Grant County line, through Ritzville and eastward.

The railroad was envisioned as an alternative to the high monopolistic rates of the Oregon Steam Navigation Company. The Northern Pacific Railway built its road across eastern Washington in the early eighties. In 1886 the Oregon Improvement Company (financed by the Oregon Railway and Navigation Company) built a branch line through the southeastern part of Adams County connecting Moscow, Idaho Territory and Connell, in Franklin County, Washington Territory. Overflow waters from Washtucna Lake subsequently destroyed sections of the road, and it was abandoned. Rails between Kahlotus and Connell were taken up but used later when trackage was laid in Washtucna Coulee. The Chicago, Milwaukee, St. Paul and Pacific Railroad was completed in 1909 and has approximately 80 miles of track in the county, which it traverses from east to west. Ralston, Roxboro, and Othello came into being as a result of this construction. Domestic goods imported into eastern Washington were as expensive as exported ones. Mr. L. Lommason of Adams County received some salt in 1885 from Chicago, valued at $24. Freight charges amounted to an additional $79.80.[42] Clark Russell, another Inland Empire farmer, imported a Ball's thresher from Portland in 1889. Boxed and hauled by wagon around the Cascades of the Columbia River, the thresher, with freight charges, came to $1400.00.[43]

Pioneer Problems

At first pioneers maintained themselves only slightly above a subsistence level of existence. Lack of water for crops and house and the lack of fuel were serious impediments. A number of early settlers in the panhandle region of Adams County journeyed to Scootenay Springs for water. Wood in quantity was not plentiful and had to be transported from the far away mountains. Houses of any type of lumber were expensive and prohibitive for most immigrants. Many lived in wagons or tents at first. When boards of any type were used, the hastily constructed shacks were frequently battened with whatever was available, usually newspapers.[44] Most furnishings were sparse and crudely made; labor and materials could be given only to the very essential pieces.

Initial harvests of grain were gratifying, but wheat farmers in northern parts of the county-to-be had difficulties using the soil to reap maximum yields. Inadequate machinery and unsuitable methods were demonstrated by David Buchanan, who had experimented with wheat crops on his Wisconsin farm before removing to Adams County. Using a three-horse team he ploughed more carefully and deeply. Local farmers took note, and improved crops were soon evident. Perhaps the most significant discovery regarding wheat productivity was that which overcame decades of eastern farming attitudes. Realization that hill lands were fertile proved significant.

Farmers had additional problems. In certain localities potato plants were destroyed by large jack rabbit populations. Bounties were offered for squirrel scalps between 1887 and 1894 while rabbit drives depopulated the white-tailed jacks. The problem, however, was not solved for soon black-tailed jacks appeared in alarming numbers. Before the turn of the century strychnine was resorted to with some success.

Water

Low annual precipitation, coming mostly in winter, was a new experience for transplanted Midwestern farmers, and disappointingly, the then popular adage—that cultivation induced rainfall—was not holding true. With precipitation well distributed throughout the year in the Midwest, this supposition had been easy to assume. New settlement and newly ploughed fields followed in rapid succession—and the rains came. That they came regardless of the ploughed fields was perhaps not observed sufficiently or recorded accurately enough to impress the geographically unsophisticated of the era. Symons, the Army explorer, attributed the westward progress of settlement as the responsible agent for increased rainfall; promotional railroad literature widely quoted material claiming that increased populations, and cooling by cultivation, brought springs from hillsides and larger streams. Ruffner reported in 1889 that moisture on the productive Columbia Plateau must come "partly from the deposition of moisture by the sea air which comes through the gap in the Cascade Mountains and penetrates the deep, loose soil."[45]

As weather was the nemesis of the cattleman, the lack of moisture was a major problem for the farmer. Settlement in the interior regions of eastern Washington was impeded by a scanty water supply. Adams County has only three streams which carry water the entire year—Cow Creek, McElroy Creek, and Crab Creek. Although the Palouse River forms the county's southeastern border, its waters were not used for irrigation.

As early as 1875 diversion of Palouse River water down Washtucna Coulee was discussed. Feasibility surveys in the 1890's resulted in canal and dam construction. However, enormous costs, estimated at six million dollars for concrete linings to avoid seepage, caused abandonment of the project in 1906.[46] Among Washtucna residents plans circulated to irrigate 4000 nearby acres from the Palouse River in 1900.[47] Another project to tap Colville Lake and dig a ditch along the Northern Pacific tracks to Lind in 1904 was abandoned. A proposed Crab Creek reservoir as well as plans to generate power at Palouse Falls created excitement some years later.

There were some successful early attempts at irrigation in Adams County. In 1899,

TABLE 7. Irrigated lands.*

Year	Acres	Number of farms
1896	900	——
1899	423	12
1909	1,523	20
1919	943	——
1920	——	8
1929	1,183	22
1950	1,237	11
1954	10,959	127
1959	48,280	321
1964	76,116	341

* Censuses of the State of Washington pertaining to agriculture, 1890 through 1964.

12 farms had a total of 423 acres under irrigation. By 1909, eight more farms were added to irrigation operations, and these had 1523 acres of cropland receiving water artifically. (See Table 7.)

Insufficient water supplies were long recognized as a serious impediment by explorers, scientists, and government officials. Few springs exist in the region, and hope

for wide-scale artesian wells did not materialize. Frequently, before reaching the land where their dreams would be fulfilled, pioneers had received a somewhat different picture of the situation as the following excerpt from the *West Shore* indicates:

> The whole country is well adapted to the storage of water falling upon it and percolating through small fissures and interstices to the great fissures and creeks below, to again reach the surface in numerous springs. Nowhere will wells have to be sunk more than twenty five to thirty feet while most of them will secure abundance at much less depth.[48]

To try to alleviate the water problem, the 1886 Territorial Legislature appropriated $6000 to sink artesian wells in eastern Washington. The next year Governor Semple reported to the Secretary of the Interior that $2500 had been set aside for experimentation with artesian wells in Adams County. With the exception of a six-mile square area, the venture was unsuccessful, but the necessity for water in the dry months generated the idea of reservoirs as a means of conserving run-off waters in the winter and spring. Nonetheless, the general water problem concerned the United States Congress and the unique phenomenon of successful wheat cultivation without summer rains so intrigued that body that a resolution was passed, the results of which were published in Green's Report of 1888.

A geological survey in 1892 determined that extensive irrigation from artesian waters was not feasible. At best only a few acres would benefit from such wells. Despite popular reports that good water could be obtained at moderate depths, wise counsel suggested canals, water-storage reservoirs, and pumping for extensive irrigation.

One attempt at solution of the problems was made by the Adams County Commissioners in 1892 when they considered a rain-making proposition by the Swisher Rain Company. The firm was to "make a rain test in an amount of not less than one half inch at some point within a radius of thirty five miles of the point of operation, for the sum of $600."[49] Interest in the project dissolved when the rainmakers failed to appear for the test.

New Immigration

Economic disturbances throughout the country generally depressed the flow of immigrants westward during the 1890's. In fact, many farmers and shopkeepers left eastern Washington. A rainy harvest season in 1893 plunged many to the point of despair. However, in 1897 and 1898 bumper crops were harvested, proving that wheat farming in the county was profitable. For the first time, too, wheat farmers occupied more of the county than did cattle ranchers. Those bountiful crops figured prominently in the tremendous influx of new settlers after the turn of the century.

It was then that previously ignored drier lands in the Big Bend region opened, and the Adams County population grew to 4480. Settlers were forced to consider these "less desirable" places when choice lands in the county had been occupied. Dry-farming methods on an extensive scale were introduced in these scantily watered areas and brought an enormous expansion of wheat production. Here, too, farming became a large-scale mechanized operation. By 1904 Adams County no longer offered land for homestead entry.

Conclusion

During the period of cattle-ranching dominance, Whitman County (then including Adams) had no towns. Walla Walla was the source of supplies. By the Tenth Census (1880) four towns sprang into existence—Colfax, Palouse City, Farmington, and

TABLE 8. Farms in Adams County.*

Year	Number of farms	Average size of farms	Acres in farms	Per cent of county area in farms
1890	399	352	140,301	11.6
1900	783	631.5	494,452	40.2
1910	1,263	775.5	979,455	80.0
1920	1,084	865.7	938,395	76.7
1930	818	1,230.5	1,006,582	82.3
1935	775	1,295	977,519	79.9
1940	651	1,477	961,557	79.3
1945	597	1,767.6	1,055,281	87.0
1950	602	1,834.6	1,104,425	91.1
1954	639	1,616.7	1,033,088	85.2
1959	786	1,370.2	1,076,960	88.8
1964	744	1,616.6	1,202,769	99.2

* Censuses of the State of Washington pertaining to agriculture, 1890 through 1964.

TABLE 9. Value of farm lands and buildings.*

Year	Average per farm	Average per acre	Value of all farmland and buildings
1890	———	———	$ 4,761,011
1900	$ 4,963	$ 7.86	3,885,950
1910	23,525	24.93	26,103,779
1920	31,767	36.70	34,435,448
1930	28,096	22.83	22,982,466
1940	32,112	21.74	20,904,693
1950	105,310	54.57	63,396,620
1954	130,677	82.50	83,502,603
1959	133,626	102.15	105,030,036
1964	183,785	113.96	

* Censuses of the State of Washington pertaining to agriculture, 1890 through 1964.

Spangle—reflecting a change in consumer orientation. Farms in Adams County numbered 399 at the Eleventh Census, doubled in the subsequent decade, and tripled the original amount by 1910. Peak population of the pioneer period came that year when 10,920 persons resided in the county. For several decades thereafter the number of farms decreased. Modern machinery and more efficient farming techniques, however, have enabled the individual farmer to cultivate more land and reap better yields. (See Tables 8 and 9.)

As each tiny cluster of houses and stores took root, townsfolk entertained dreams of their town emerging as the major regional metropolis. Inglorious beginnings as a railroad water-tank stop or the crossroads of early routes were of little importance. Today, remains of blossoming towns that withered before fulfillment are scattered throughout the county. In some Adams County towns—Schoonover, Batum, Paha, Benge, Ralston, Griffith Corners—a few residents remain among dying remnants of days of promise. Out in the lonely places among the desolate scabrock a variety of animal life moves among shadowy memories in deserted homesteads and decaying orchards, sad testimonies to dreams that died.

Farming and stock raising today produce the major income of the county. Irrigated farms in western sections reap a number of different crops—alfalfa, hay, dry peas, dry beans, potatoes, field corn, sugar beets, onions, peppermint. Othello, in the county panhandle, is the fastest-growing community in Adams County. Although regional population growth has provided markets for the increasing productivity, the bulk of

the products is shipped far beyond the borders of the region. Unless there occurs a momentous impetus for change, it is most likely the county will continue in this manner for some time to come.

References

1. U.S. Congress, House, Letter from the Secretary of the Army, *Columbia River and Tributaries, Northwestern United States,* 8 Vols., Vol. III (81st Cong. 2nd sess., House Doc. # 531. Washington: Government Printing Office, 1952), p. 1094.
2. Richard F. Flint, Summary of Late Cenozoic Geology in Southeastern Washington, *American Journal of Science,* XXXV (March, 1938), p. 223.
3. C. D. Campbell, personal communication, Department of Geology, Washington State University, Pullman, Washington (May 25, 1969).
4. Thomas W. Symons, U. S. Congress, Senate, *Report on an Examination of the Upper Columbia River and the Territory in its Vicinity in September and October, 1881* (47th Cong. 1st sess., Sen. Ex. Doc. 186, 1882), p. 133.
5. *Columbia River and Tributaries, Northwestern United States,* p. 971, Vol. III.
6. Earl L. Phillips, *Washington Climate* (Washington State University Agricultural Extension Service, Pullman, Washington, 1965 ?), p. 9.
7. Phillips, *Washington Climate,* p. 14, p. 26.
8. Phillips, *Washington Climate,* p. 15.
9. William S. Lewis, ed., A Pioneer of the Spokane Country, *Washington Historical Quarterly,* Vol. 7 (October, 1916), p. 274.
10. Phillips, *Washington Climate,* p. 10.
11. W. H. Ruffner, *A Report on Washington Territory* (n.p., New York, Seattle, and Lake Shore and Eastern Railway, 1889), p. 84; D. P. Ballard, *Washington Territory and the Far Northwest* (Chicago, Ballard & Company, 1889), p. 9.
12. Clinton A. Snowden, *History of Washington,* 4 Vols. (New York, Century History Company, 1909), Vol. 4, pp. 90-91.
13. Eugene S. Dzuedzic, *Land Use and Wildlife on Farms of Southeastern Washington* (unpublished Master's thesis, State College of Washington, 1951), p. 10.
14. Dzuedzic, *Land Use and Wildlife on Farms of Southeastern Washington,* p. 15.
15. Helmut K. Buechner, Some Biotic Changes in the State of Washington, particularly During the Century, 1853-1953, *Research Studies of the State College of Washington,* XXI, No. 2 (June, 1953), pp. 166-178.
16. Cotton, *Forage Problems of Eastern and Central Washington* (unpublished Master's thesis, State College of Washington, 1904), p. 11 quoted in Boyce, *A History of the Beef Cattle Industry in the Inland Empire.*
17. Dzuedzic, *Land Use and Wildlife on Farms of Southeastern Washington,* pp. 26-31.
18. Bruce Stallard, *Archaeology in Washington,* Division of Mines and Geology, Information Circular No. 30, State of Washington (Olympia, 1958), p. 27.
19. Richard Daugherty, Barbara Purdy, & Roald Fryxell, The Descriptive Archaeology and Geochronology of the Three Springs Bar Archaeological Site, Washington, *Laboratory of Anthropology, Report of Investigations No. 40* (Washington State University, Pullman, 1967), p. 107.
20. Bureau of American Ethnology, *Annual Report to the Secretary of the Smithsonian Institute,* No. 45 (Washington: Government Printing Office, 1927-1928), p. 37.
21. Bureau of American Ethnology, *Annual Report to the Secretary of the Smithsonian Institute,* No. 45 (Washington: Government Printing Office, 1927-1928), p. 344.
22. Elkanah Walker, Letter to Rev. D. Greene, Tshimiakain, October, 1841, Vol. 138, letter 78 (in Clifford M. Drury Manuscript, *Letters of Elkanah Walker* and Related Papers), pp. 69-70.
23. *Reports of Explorations and Surveys to Ascertain the most Practicable and Economical Route for a Railroad from the Mississippi River to the Pacific made under the Direction of the Secretary of War in 1853-55,* Vol. 12, Book 1 (Washington: Government Printing Office), p. 199.
24. *Railroad Surveys,* Vol. 12, Book 1, pp. 329-330.
25. Charles M. Gates, ed., *Messages of the Governors of the Territory of Washington to the Legislative Assembly, 1854-1889* (Seattle: University of Washington Press, 1940), pp. 23-25.
26. Charles M. Gates, ed., *Messages of the Governors of the Territory of Washington,* p. 34.
27. Frank T. Gilbert, *Historic Sketches of Walla Walla, Columbia, and Garfield Counties, W. T., and Umatilla County, Oregon* (Portland: A. G. Walling, 1882), pp. 223-224.
28. William S. Lewis, *The Story of the Early Days in the Big Bend Country* (Spokane: W. D Allen, 1926), pp. 33-35.
29. Donald Meinig, *Environment and Settlement in the Palouse, 1868-1910* (unpublished Master's thesis, University of Washington, 1950), pp. 24-26.
30. *Adams County Pioneer Edition* (Ritzville, Washington), September, 1949, p. 43.
31. *The West Shore,* April, 1883 (Vol. IX, No. 4), p. 73.
32. John Mullan, *Miners and Travelers Guide to Oregon, Washington, Idaho, Montana, Wyoming, and Colorado, via the Missouri and Columbia Rivers* (New York: William M. Franklin, 1865), pp. 59-60.
33. William S. Lewis, *Early Days in the Big Bend Country,* p. 18.

34. William S. Lewis, *Early Days in the Big Bend Country,* p. 8; *Adams County Pioneer Edition,* September, 1949.
35. William H. Brewer, Report on the Cereal Production of the United States in "Report on the Productions of Agriculture, 10th Census," Department of the Interior, Census Office, *Agriculture* (Washington: Government Printing Office, 1883), p. 371-553.
36. Arthur J. Brown, *Means of Promoting Immigration to the Northwest and Washington to 1910,* Master's Thesis, University of Washington, 1942, p. 29.
37. Arthur J. Brown, *Means of Promoting Immigration to the Northwest and Washington to 1910,* p. 32.
38. Todd V. Boyce, *A History of the Beef Cattle Industry in the Inland Empire,* Master's Thesis, State College of Washington, 1937, p. 61.
39. W. H. Ruffner, *A Report on Washington Territory,* pp. 81-82.
40. *The Spokane Spokesman* (Spokane, Washington), January 1, 1892, p. 27.
41. C. S. Kingston, ed., The Northern Overland Route in 1867: Journal of Henry Lueg, *Pacific Northwest Quarterly* (Seattle: University of Washington Press, July, 1950), p. 248. Frank T. Gilbert, *Historic Sketches of Walla Walla, Whitman, Columbia and Garfield Counties, W. T. and Umatilla County, Oregon,* p. 433.
42. *Adams County Record* (Ritzville, W. T.), November 17, 1885.
43. Helga Travis, *Golden Bonanza* (Prosser, Washington, 1963), pp. 15-16.
44. Works Project Administration, *Told By the Pioneers,* 3 Vols. (1937-1938), Vol. 3, p. 119.
45. W. H. Ruffner, *A Report on Washington Territory,* pp. 85-87.
46. *Adams County Pioneer Edition,* p. 25.
47. *Adams County Pioneer Edition,* p. 7.
48. *The West Shore,* April, 1883.
49. *Adams County Pioneer Edition,* p. 64.

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Chemical Properties of the Arid Soil Organic Fraction

The organic fraction of soils of the humid and subhumid regions of the world is known to exert an influence on soil transformations which far exceeds what might be deduced from its proportion by weight. The soil organic matter contributes substantially to soil sorption of nutrient elements (Wiklander, 1964), pesticides (Armstrong *et al.,* 1967; Wildung *et al.,* 1968a) and radionuclides (Mortensen and Marcusiu, 1963; Nishita *et al.,* 1956). Furthermore, the soil microflora are often directly involved in transformations of these materials (Alexander, 1961; Crafts, 1961; Stevenson, 1965). However, information regarding the mechanisms and extent of the participation of the soil organic fraction and the soil microflora in these phenomena is far from complete, particularly in arid climates.

The lack of information regarding the chemical properties of the arid soil organic fraction is presumably due to the inherent low concentrations of organic matter in these soils. However, in arid soils low in clay minerals, the organic fraction, due to its high charge density, may assume, in addition to its functions in the flow of energy and cyclization of C and N, an important role in exchange reactions which govern the fate of inorganic and organic ions in soil. With increased dependence upon arid lands by a growing world population, an integrated approach must be taken to elucidate the role of soil in the arid land ecosystem. In 1967, the United States Atomic Energy Commission set aside 210 square km of the Hanford Reservation at Richland, Washington, as an arid land ecology (ALE) reserve. This arid shrub-steppe region has been relatively undisturbed for over 25 years and present access is strictly controlled. Over a distance of approximately 13 km the elevation increases up a north-facing slope from about 155 m on the basal plains to more than 1060 m along the crests of what are known as the Rattlesnake Hills, thus providing a unique area for the study of the arid land ecosystem, including the biochemistry of the arid soil organic fraction, over a broad altitudinal range.

As the first phase in a continuing program to determine the role of the soil in the flow of energy, the cyclization of nutrients, and the behavior of soil-deposited pollutants within the arid land ecosystems on the ALE reserve, this study was designed to (1) develop and evaluate methodology for the chemical characterization and study of arid soils, (2) characterize intact arid soils representing several plant-soil associations over a broad altitudinal range as to physicochemical properties, and (3) isolate and characterize chemically arid soil humic colloids as to elemental composition and Sr ion exchange capacity.

Materials and Methods

In order to evaluate possible changes in the chemical properties of the soil organic fraction as influenced by changes in ambient temperature and moisture, soil humic acids were isolated from surface (0-8 cm) soils sampled in the fall along a 13-km altitudinal transect from 155 to 1060 m elevation. The sampling sites on the ALE Reserve were selected on the basis of their altitude, vegetation and surface-soil characteristics. The principal characteristics of the sampling sites are described in Table 1.

The primary influences of altitude on soil organic matter deposition and transformations may be expected to arise from differences in vegetation, temperature, and moisture. *Artemisia tridentata* (Big sagebrush) is the principal overstory shrub species throughout the altitudinal sampling range (155 to 1060m) whereas the grass understory consists primarily of *Bromus tectorum* at the lower elevations (< 180m), *Poa secunda* at approximately 180 to 270m, and *Agropyron spicatum* at elevations above 270m (Table 1).

The soils (Table 1) at the lower elevation (Burbank ls, Ephrata 1) developed in sand overlying gravelly river deposits. At the higher elevations (Warden sl, Ritzville sil, and Lickskillet l) the parent material was primarily aeolian silt (Hajek, 1966). The pH of the untreated soils was measured by the glass electrode method on a thin aqueous paste equilibrated 30 minutes. Particle-size composition was determined by centrifugation techniques according to the method of Jackson (1956).

Soil humic acids, high-charge density extractives of the soil organic matter, were isolated from soils after (1) treatment (3 times) of soil samples (3-5 kg) with HCl (0.1*N*) at a 3/2 HCl/soil ratio to remove carbonates and undecomposed plant fragments by flotation, and (2) pre-extraction with a 1/1 benzene/ethanol mixture for eight hours in a Soxhlet apparatus to remove fats, waxes, resins, and tannins which might contaminate the humic acid. The benzene/ethanol mixture was saved for elemental analysis. Humic acids were isolated from the residue by NaOH dissolution as described by Wildung *et al.* (1965).

The initial crude humic acid preparations were purified by three repeated dissolutions and precipitations and finally dialyzed against distilled H_2O to remove excess salts. Purified humic acids were chemically characterized as to elemental composition (C, H, and N) and pH dependent cation (Sr) exchange capacity (CEC), a relative measurement of the affinity of the organic functional groups for cations in solution.

The C, H, and ash contents of intact soils and soil humic colloids were measured as described by Wildung *et al.* (1970), whereas N was determined by the Dumas method as described by Welcher (1966).

The CEC of soils and soil humic acids were measured by a modification of the method described by Okazaki *et al.* (1962). Air-dry soil samples (4.000 to 6.000 g), of known moisture contents, were cation saturated at pH 4.0 and pH 7.0 using a buffer solution containing $Sr(OAc)_2$ (0.8*N*) and $SrCl_2$ (0.2*N*) spiked with ^{85}Sr (10,000 dpm/ml) and adjusted to the appropriate pH with dilute HCl or $Sr(OH)_2$. Cation saturation involved equilibration of the soil by mechanical shaking (3 hrs) with the buffer solution (30 ml) in tared 50-ml centrifuge tubes. Following initial equilibration, centrifugation, and decantation of the supernatant buffer solution, the samples were re-equilibrated (20 min) with a fresh increment (30 ml) of Sr buffer solution. The short equilibrations were repeated an additional five times. Following

TABLE 1. Description of arid land soils.

Classification	Vegetative understory	Elevation	pH	Contents* of Organic carbon	Sand (> 50μ)	Silt (50 to 2μ)	Clay (< 2μ)	CEC at pH 7.0
		M		%				meq/100g
			Burbank ls					
Typic Torripsamment	*Bromus*	155	6.9	0.46	76.8	16.8	6.4	11.2
			Ephrata l					
Andic Mollic Camborthid	*Bromus*	155	7.4	0.43	44.2	47.1	8.7	16.1
			Warden sl					
Andic Mollic Camborthid	*Poa*	190	7.0	0.52	55.5	34.1	10.4	18.1
			Ritzville sil					
Andic Aridic Haplustoll	*Agropyron*	445	6.2	0.66	23.3	64.1	12.6	22.5
			Lickskillet l					
Lithic Haplustoll	*Agropyron*	940	6.2	3.62	42.6	41.1	16.3	40.3

* Percent organic carbon based on total soil, other values on total minerals.

Sr saturation, the samples were equilibrated during 20-min shaking periods a total of six times with diluted buffer solution (0.1*N*) to reduce the concentration of salts retained by the sample as buffer solution. After final centrifugation the tube and its contents were weighed accurately. Total Sr was displaced from the sample and the buffer solution it retained by 6 (20 min) extractions with *N* $Mg(OAc)_2$ adjusted to pH 5.0 with HOAc. The Sr concentrations in a fresh increment of the 0.1*N* buffer solution and in the combined $Mg(OAc)_2$ extracts (containing total Sr) were calculated from measurement of ^{85}Sr specific activity. The quantity of buffer solution retained by the sample after the final equilibration was determined gravimetrically. A knowledge of the quantity of wash solution retained by the sample and the concentration of Sr in the wash solution (soluble Sr) allowed calculation of exchangeable Sr by subtraction of soluble Sr from total Sr.

The CEC of soil humic acids (0.0250 to 0.0500g) were determined in a similar manner except saturating, washing, and displacing solutions were decreased to 10 ml and plastic 50-ml centrifuge tubes were employed. The plastic centrifuge tubes were lighter in weight than the glass tubes, thereby minimizing weighing errors.

Results and Discussion

The principal objectives of this investigation were to (1) characterize physicochemically representative soils of the ALE Reserve and (2) define the chemical nature of the arid soil organic fraction to provide insight into its role in arid soil chemical transformations.

Intact soils were characterized as to contents of C, alcohol-benzene soluble components, humic acids, and CEC. Isolated humic acids were characterized as to contents of C, H, N, and ash and as to pH-dependent CEC.

Established techniques for the characterization of the soil organic fraction proved generally applicable to the arid soil system when sample size was increased to provide sufficient materials for adequate analytical resolution and precision.

Chemical Properties of Intact Soils

The C content of the intact soils showed an overall increase with increased elevation (Table 1) likely reflecting increased soil organic matter contents as a result of (1) increased plant understory biomass and soil deposition of organic matter with increased rainfall and (2) decreased soil organic matter degradation rate with decreased mean ambient temperature (Rickard, 1968; Hinds and Thorp, 1969). The increased soil C content with higher elevation may also reflect a larger quantity of aromatic substances, resistant to microbial decomposition, deposited on the soil as lignin in associated grass tissues. Previous investigations (Wildung *et al.,* 1968b) have shown that the lignin content of mature *Bromus, Poa,* and *Agropyron* tissue amounted to 2.7, 3.6, and 4.5 percent, respectively. Assuming total biomass deposited on the soil by the individual grasses was equivalent, the quantity of lignin reaching the soil in the form of grass tissue should be proportional to the lignin content of the grass tissues and therefore increase upslope.

The soil clay contents ranged from 6.4 to 16.3 percent and also increased upslope (Table 1). Cation exchange capacities (Table 1) of the Burbank, Ephrata, Warden, Ritzville, and Lickskillet soils at pH 7.0 were 11.2, 16.1, 18.1, 22.5, and 40.3 meq/100g, respectively, thereby increasing with increased soil clay and organic C content. The

observed increase in CEC resulted from increased surface area and solid-phase coulombic charge associated with higher concentrations of colloidal mineral and organic matter.

Chemical Properties of Soil Humic Colloids

The C removed from soil as humic colloids or accessory (alcohol/benzene soluble) components ranged from 4.0 to 16.5 and 1.7 to 7.8 percent, respectively (Wildung *et al.,* 1968b). On a total weight basis, yields of NaOH and alcohol/benzene soluble materials from soils were less than 0.5 percent and therefore comparisons of the yields of soil extractives would be tenuous. Yields of humic components were substantially increased by removal of CO_3-C prior to extraction. The C, H, and N contents of isolated soil humic colloids were quite similar and ranged from 54.3 to 58.1, 5.7 to 6.2, and 4.8 to 5.8 percent, respectively (Table 2). These data are comparable with values reported by previous investigators (Kononova, 1966; Wildung *et al.,* 1970) for humic components from a wide variety of mineral soils developed under different climatic conditions.

Although elemental compositions of the humic colloids were similar, the Warden sl and Ritzville sil humic acids exhibited significantly higher C and N contents and lower C/N ratios than either the Burbank or Ephrata humic colloids, whereas the Lickskillet humic colloid gave intermediate values (Table 2). The H contents were quite similar with the maximum difference occurring between the Warden (6.2% H) and Lickskillet (5.7% H) samples. The C/H ratios were also similar ranging from 9.1 (Burbank ls) to 9.9 (Lickskillet l).

Cation exchange capacities of soil humic colloids (Table 2) at pH 4.0 and 7.0 ranged from 76 to 196 and 190 to 270 meq/100g, respectively. Thus, the CEC of soil humic acids were markedly pH-dependent, substantiating previous evidence that the CEC of humic acids arises from the negative charge present on the conjugate base of an organic acid after ionization of H. The CEC of the Warden humic acid amounted to over twice that of either the Burbank or Ephrata humic acids at pH 4.0. The Ritzville and Lickskillet were intermediate between the Warden and the Burbank and Ephrata humic acids at the low pH. At pH 7.0, the Warden and Burbank samples gave the highest CEC; the Ritzville and Lickskillet humic acids exhibited the lowest values and the Ephrata occupied an intermediate position.

The comparatively high CEC of the Warden humic acid, particularly at pH 4.0, may reflect the high CEC of the associated plant lignin, *Poa* at 7.0 (Wildung *et al.,*

TABLE 2. Elemental composition and cation exchange capacity of soil humic acids.

Soil humic acids	Ash	Contents of			Ratio of		CEC	
		C	H	N	C/N	C/H	pH 4.0	pH 7.0
	%	% of dry, ash-free sample					meq/100g	
Burbank ls	1.9	54.3	6.0	4.8	11.4	9.1	93	270
Ephrata l	12.4	55.6	5.8	4.9	11.3	9.6	76	232
Warden sl	1.6	58.1	6.2	5.6	10.3	9.3	196	260
Ritzville sil	2.9	57.8	6.1	5.8	9.9	9.4	132	190
Lickskillet l	1.2	56.6	5.7	5.3	10.8	9.9	117	200

1968b). It may be speculated that the *Poa* lignin contains a larger number of acidic groups ionizing near pH 7.0 than the other lignins, and during soil decomposition these groups are strengthened, resulting in a humic acid comparatively higher in CEC at pH 4.0.

The present investigations have formed a basis for future study of the flow of energy and the influence of the organic fraction on the behavior of organic and inorganic ions in arid soils. Immediate future investigations will be oriented toward (1) elucidation of the factors affecting the rate of decomposition of untreated native plant tissue in arid soils, and (2) isolation of native organo-clay complexes and determination of their role in ion retention.

Summary

As part of a continuing program to determine the role of soil in the flow of energy and cyclization of nutrients within an arid land ecosystem, these investigations were designed as an initial phase in the elucidation of the chemical and biological properties of the soils on the Arid Land Ecological Reserve at Hanford, Washington. Representative arid land soils were characterized as to pH, contents of organic C, sand, silt, clay, and cation (Sr) exchange capacity (CEC). Soil humic acids, amorphous, high molecular weight, and high-charge density organic colloids were isolated from representative soils and compared chemically as to elemental composition and pH-dependent CEC.

Techniques established for isolation and characterization of soil humic colloids from soils in humid and subhumid regions of the world generally performed well when applied to arid soils provided initial soil sample size was increased to allow adequate analytical resolution and precision.

The C and clay contents of untreated soils ranged from 0.43 to 3.6 percent and from 6.4 to 16.3 percent, respectively, and increased with sample site elevation. The increase in organic C content upslope apparently reflects (1) increased plant understory biomass and soil deposition of organic matter with increased rainfall, (2) decreased soil organic matter degradation rate with decreased mean ambient temperature, and (3) increased grass lignin content.

The soil CEC increased with increased C and clay contents as a result of increased surface area and solid phase coulombic charge associated with higher concentrations of colloidal mineral and organic matter.

The yield of soil humic colloids, based on the C content of the intact soil, ranged from 4.6 to 16.6 percent. The CEC of soil humic colloids were markedly pH dependent ranging from 76 to 196 meq/100g at pH 4.0 to 190 to 270 meq/100g at pH 7.0, indicating the presence of a number of acidic functional groups capable of bonding the index cation, Sr.

Elemental composition and CEC of the arid soil humic acids were similar to analogous isolates from humid regions. The chemical properties of arid soil humic acids were quite uniform regardless of changes in altitude or vegetative type.

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Literature Cited

Alexander, M. 1961. Introduction to soil microbiology. John Wiley and Sons, Inc. New York, N.Y.

Armstrong, D. E., G. Chesters, and R. F. Harris. 1967. Atrazine hydrolysis in soil. Soil Sci. Soc. Amer. Proc. 31: 61-66.

Crafts, A. S. 1961. The chemistry and mode of action of herbicides. Interscience, New York, N.Y.

Hajek, B. F. 1966. Soil survey. Hanford project in Benton County, Washington. BNWL-243. Pacific Northwest Laboratory, Richland, Washington.

Hinds, W. T., and J. M. Thorp. 1969. Biotic and abiotic characteristics of the microclimatological network on the arid lands ecology reserve. BNWL-SA-2733. Pacific Northwest Laboratory, Richland, Washington.

Jackson, M. L. 1956. Soil chemical analysis—advanced course. Published by the author, Dept. of Soils, University of Wisconsin, Madison, Wisconsin.

Kononova, M. M. 1966. Soil organic matter. Pergamon Press, Inc., New York, N.Y.

MacRae, I. C., and M. Alexander. 1965. Microbial degradation of selected herbicides in soil. J. Agr. Food Chem. 13:72-76.

Mortensen, J. L., and E. C. Marcusiu. 1963. Fission-product-soil organic matter complexes: I. Strontium-90 (Yttrium-90) in water extracts and HCl hydrolysates of soil. Soil Sci. Soc. Am. Proc. 27:653-656.

Nishita, H., B. W. Kowalewsky, and K. H. Larson. 1956. Influence of soil organic matter on mineral uptake by barley seedlings. Soil Sci. 82:307-318.

Okazaki, Rose, H. W. Smith, and C. D. Moodie. 1962. Development of a cation-exchange capacity procedure with few inherent errors. Soil Sci. 93:343-349.

Rickard, W. H. 1968. Field observations on the altitudinal distribution of the side-blotched lizard. Northwest Sci. 42:161-164.

Stevenson, I. L. 1965. Biochemistry of soil. *In* F. E. Bear [ed.], Chemistry of the soil. Reinhold Publishing Corp., New York, N.Y.

Stotsky, G. 1965. Microbial respiration. *In* C. A. Black [ed.], Methods of soil analysis. Part 2. Chemical and microbiological properties. American Society of Agronomy Inc., Madison, Wisconsin.

Welcher, F. J. [ed.]. 1966. Standard methods of chemical analysis. Vol. III. Instrumental methods. D. Van Nostrand Company, Inc. Princeton, New Jersey.

Wildung, R. E., G. Chesters, and S. O. Thompson. 1965. Cation exchange capacity of plant lignins and soil humic colloids as affected by pH and hydrolysis error. Soil Sci. Soc. Am. Proc. 29:688-692.

Wildung, R. E., G. Chesters, and D. E. Armstrong. 1968a. Chloramben (Amiben) degradation in soil. Weed Sci. 8:213-225.

Wildung, R. E., G. Chesters, and D. E. Behmer. 1970. Alkaline nitrobenzene oxidation of plant lignins and soil humic colloids. Plant and Soil 32:221-237.

Wildung, R. E., B. F. Hajek, and K. R. Price. 1968b. Chemical characterization of the arid soil organic fraction. Comparative chemical properties of plant lignins and soil humic colloids. BNWL-SA-982, Pacific Northwest Laboratory, Richland, Washington.

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Influence of Douglas-fir Seedling Height on Browsing by Black-Tailed Deer

Damage by black-tailed deer (*Odocoileus hemionus columbianus*) to Douglas-fir (*Pseudotsuga menziesii*) varies chiefly in response to the tree's acceptability and availability as a browse plant. Reducing palatability of seedlings and saplings by any reasonable means, therefore, may effectively moderate damage. Treating seedlings with chemicals, one route to this end, remains ineffective for controlling damage by deer in forest plantations. Other avenues, such as exploiting inherent qualities of Douglas-fir seedlings themselves, merit detailed study. Naturally occurring variations within the species may include palatability differences that affect use by deer or other animals in the field.

To discover if Douglas-fir seedlings from widely separated provenances might evoke varying feeding responses in deer under controlled conditions, an exploratory trial was made during the winter of 1965-66 with planting stock from five seed sources in western Washington. Preliminary results revealed that feeding preference differed markedly among the races tested. Further testing and analysis showed that preferences were strongly linked to small variations in seedling height—independent of seed origin.

Pen Trials

Testing followed general procedures described by others (Hildreth and Brown, 1955; Cardinell and Hayne, 1947) for assessing repellency of candidate chemical compounds to various lagomorphs—chiefly *Lepus* (hares) and *Sylvilagus* (rabbits). Design, layout, and analysis closely followed methods outlined by Dodge *et al.* (1967) for testing repellents against black-tailed deer and snowshoe hare (*L. americanus*). The U.S. Bureau of Sport Fisheries and Wildlife cooperated in making facilities maintained at Olympia, Washington, available for preference tests with untreated seedlings.

Untreated 2-0 Douglas-fir seedlings were exposed to voluntary feeding by black-tailed deer in two separate trials. The first test compared stock from five geographical races grown at Washington's L. T. "Mike" Webster State Forest Nursery near Olympia. The second test compared stock segregated into height groups from one of the above races. Seedlings were hoe-planted to root-collar depth in a grassy, central part of a 2.5-acre enclosure.

Deer moved freely within the enclosure, and at all times had access to cover, a maintenance diet, and some natural forage. Five animals (one buck, three does, and one fawn), randomly chosen from a herd of 22, were used to test racial effects; seven

animals (two bucks, three does, and two fawns) were later used to test height effects. The race trial began in late November 1965 and was concluded in 23 days. The height trial ran for 20 days beginning in mid-February 1966.

The same randomized block design was common to both tests, and included five treatments replicated in 10 blocks. Treatments within blocks consisted of 10 seedlings each—50 seedlings per block, or 500 seedlings per complete test. Seedlings were randomized within blocks to avoid bias from "row feeding." Spacing was 3 by 3 feet within blocks—each block arranged in five 10-seedling rows.

While exposed to deer, seedlings were checked daily, and the day of earliest browsing was noted for each seedling. Repeated browsing on the same seedlings was neither recorded nor evaluated. Examinations continued until 95 percent or more of all seedlings had been browsed.

Analysis of variance, supplemented by the Q method (Snedecor and Cochran, 1967) for comparing individual treatment means, was the basic statistical tool employed. Two measures of relative preference were used: (1) percent browsing (cumulative) as determined for each day of exposure, and (2) mean exposure in days required for all (95+ percent) seedlings to be browsed. Percentages were analyzed both in the raw form and as transformed to angles by arc sine. Since transformed and untransformed percentages gave similar results, only raw percentages are given.

Race Test

Seedlings selected for trial represented seed sources from a cross section of locations and elevations in western Washington. Racial designations were "Kelso," "Belfair," "Eldon," "Lewis," and "Glenwood" (Table 1). Nursery beds from which represen-

TABLE 1. *Race Test.* Statistical description of Douglas-fir seedlings before exposure to browsing by black-tailed deer (100 seedlings per race).

Race	Source elevation	Mean height at planting	Sampling error ($p = 0.05$)	Significant height differences ($p < 0.05$)[1]
	Feet	*Centimeters*	*Centimeters*	
Kelso	800	22.6	±.7	A
Belfair	400	21.4	±.8	A
Eldon	1,000	18.6	±.6	B
Lewis	1,000	16.1	±.7	C
Glenwood	2,500	13.1	±.5	D

[1] Means not followed by a common letter differ significantly based on 10 replicates of 10 seedlings each.

tative stock was taken were similar and had received the same regime of nursery culture. All stock was sorted and culled in accord with commercial practice.

Seedling size, as observed before testing, generally decreased with increasing elevation of seed origin. Since size might influence feeding preference, planted heights of all seedlings were recorded to the nearest centimeter. Minimal size variation within races, evidenced by relatively low sampling errors for planted height, suggested that mean heights between some races might differ significantly. Analysis showed

that only Kelso and Belfair stock, in fact, failed to differ significantly from one another (Table 1). However, the effect of height variation on preference was not clearly apparent until browsing was complete and data were analyzed.

Height Test

Effects of seedling height were also tested independently with Eldon stock. Seedlings were sorted into five height groups (100 seedlings each) with mean planting heights ranging from 10.5 to 22.5 centimeters (Table 2).

TABLE 2. *Height Test.* Statistical description of Douglas-fir seedlings before exposure to browsing by black-tailed deer (Eldon race, 100-seedlings per height group).

Height group	Mean height at planting	Sampling error ($p = 0.05$)	Significant height differences ($p < 0.05$)[1]
	Centimeters	*Centimeters*	
I	22.5	±.4	A
II	19.9	±.4	B
III	16.1	±.6	C
IV	13.3	±.4	D
V	10.5	±.4	E

[1] Means not followed by a common letter differ significantly based on 10 replicates of 10 seedlings each.

Results

Deer discriminated between seedlings from the very start. Preferential browsing was significant by the first day in the race test; by the second day in the height test (Figs. 1 and 2). The preference orders established early were generally maintained with minor variations throughout each trial.

Race Test

Seedlings from lower elevation races (Kelso and Belfair) were clearly preferred over the highest elevation race tested (Glenwood), and the difference was accentuated within the first week (Fig. 1). Maximum separation of means occurred by the 12th day —90 and 89 percent vs. 39 percent, respectively. Thereafter, differences decreased as the less preferred seedlings were eventually browsed. Conclusion of the race test permitted a more concise treatment comparison through analysis of mean exposure time required for all seedlings within a race to be browsed:

Race	Mean seedling height	Mean exposure before browsing
	(Centimeters)	(Days)
Kelso	22.6	7.4 (A)
Belfair	21.4	7.7 (A)
Eldon	18.6	9.3 (A, B)
Lewis	16.1	10.8 (B)
Glenwood	13.1	14.1 (C)

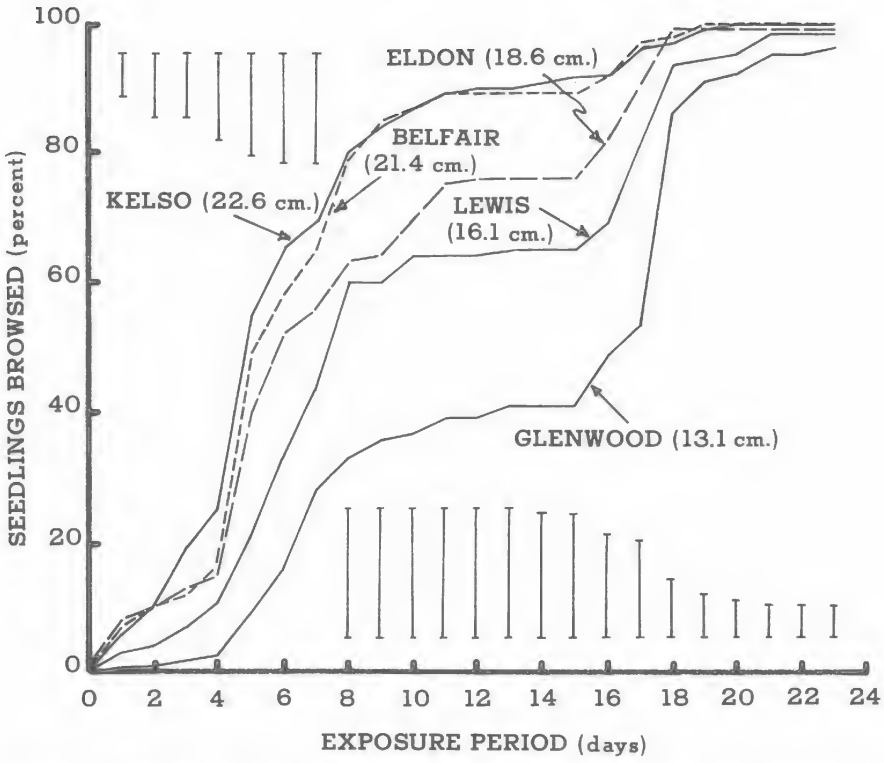

Figure 1. Browsing preference by black-tailed deer for Douglas-fir seedlings from five western Washington races. (Differences exceeding bar lengths are significant at $p < 0.05$.)

Glenwood seedlings required nearly twice as much time to be browsed as Kelso and Belfair seedlings (days not followed by a common letter significantly differ at $p < 0.05$).

The obvious correlation between seedling height and preference by deer, as measured by mean exposure before browsing, is highly significant ($r = -0.792$ with 48 df) and suggests that most of the apparent preference for certain races might be caused by the greater attractiveness of taller seedlings. Adjustment by covariance analysis of mean exposure times to an average seedling height for all races (18.4 cm) shows that height, indeed, had a powerful impact:

Race	Mean exposure before browsing adjusted to mean height
	(Days)
Lewis	9.0
Eldon	9.6
Belfair	10.0
Kelso	10.3
Glenwood	10.4

None of the differences between adjusted means was significant.

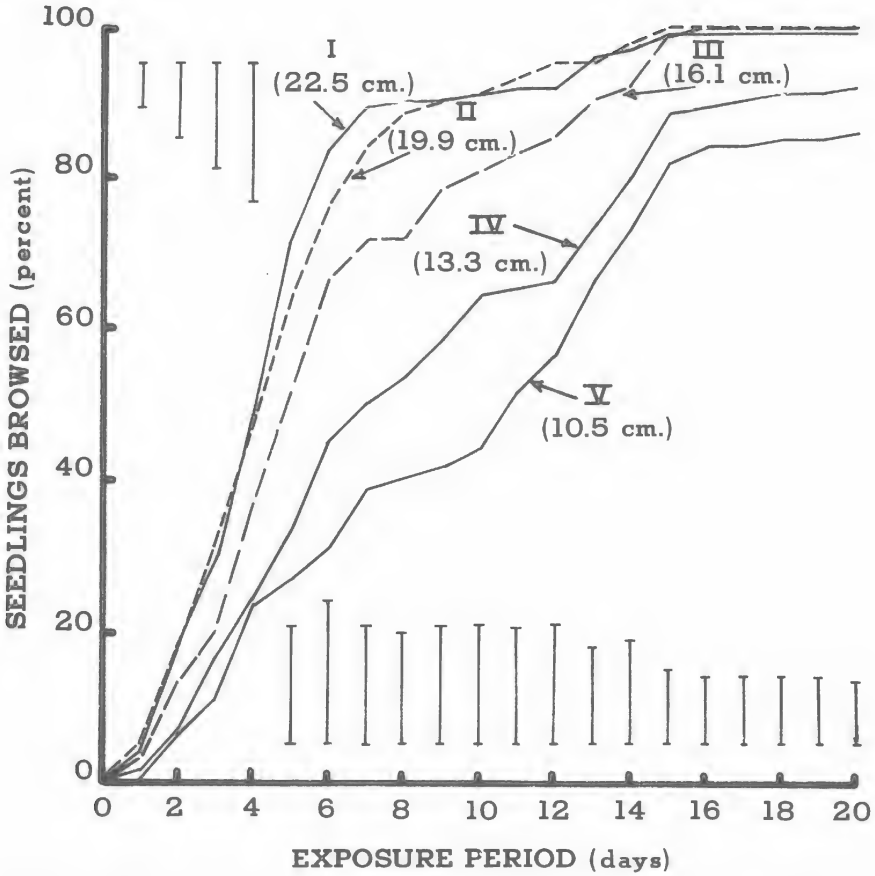

Figure 2. Browsing preference by black-tailed deer for Douglas-fir seedlings from one western Washington race (Eldon) segregated into five height groups. (Differences exceeding bar lengths are significant at $p < 0.05$.)

Height Test

The height test with Eldon stock (Fig. 2) corroborated the independent effect of height variation on deer preference within the 12-centimeter range between group means:

Height group	Mean seedling height	Mean exposure before browsing
	(Centimeters)	(Days)
I	22.5	5.2 (A)
II	19.9	5.2 (A)
III	16.1	6.6 (A)
IV	13.3	9.1 (B)
V	10.5	10.8 (C)

Again, seedlings in the two tallest groups were browsed twice as readily as those in the shortest group (days not followed by a common letter significantly differ at $p < 0.05$).

Discussion and Conclusions

Despite failure of the race trial to show clear feeding preferences by deer for seedlings from different provenances, the testing methods used appear suitable for further study of animal preference among tree seedlings of the same species. Since test animals must discriminate seedling by seedling in selecting or rejecting different genotypes, the likelihood of results having applicability under field conditions is enhanced. Also, simultaneous use of several deer in testing serves to smooth out varying feeding responses between individual animals to provide a more representative result. Further, the preceding demonstration of significant preferences between seedlings differing by less than 3 cm in height attests to the adequacy of the design.

In pen tests of short duration, the measure of preference through mean time of exposure before browsing seems at least equally suited to analysis and interpretation as browsing intensity in percent. It better reflects mean preferences shown throughout the entire exposure period. Since every seedling provides a measured value (time), rather than a binomial occurrence (browsed or unbrowsed), data transformation is unnecessary. Also, the point of peak sensitivity for analysis cannot be accidentally bypassed.

Ascribing demonstrated preferences solely to height is probably an oversimplification. The close correlation between source-related seedling heights and preferences shown does not preclude the possibility that qualitative variations also affected deer browsing. Similarly, even the independent height test with Eldon stock may have masked qualitative, height-correlated differences—*i.e.,* the taller, faster-grown seedlings may have been more palatable as well as more conveniently available. The case is convincing, however, that height at planting functions independently as a determinant of feeding preference by deer among seedlings less than 25 cm tall.

Precautions to minimize effects of height variation seem mandatory in pen testing seedlings for susceptibility to deer browsing. Though height variation may be accounted for statistically, the use of similar-sized seedlings would seem simpler and surer. In short-term pen tests this may be accomplished by deeper planting of tall seedlings to approximate the heights of shortest seedlings being tested.

The same precautions would apply to assessing field comparisons of planting stock classes that differed in size. Recent field work by the author (Dimock, 1970) has shown that 12-year-old Douglas-fir saplings growing in dense western bracken (*Pteridium aquilinum* var. *pubescens*) were browsed less frequently as their heights decreased below 4 feet. Field tests of qualitative preference by deer for seedlings of different origin or pretreatment should probably be short term. Otherwise, differences in growth rates might well make results uninterpretable.

Literature Cited

Cardinell, H. A., and D. W. Hayne. 1947. Pen tests of rabbit repellents. Mich. Agr. Exp. Sta. Quart. Bull. 29: 303-315.

Dimock, E. J., II. 1970. Ten-year height growth of Douglas-fir damaged by hare and deer. J. Forest. 68: 285-288, illus.

Dodge, W. E., C. M. Loveless, and N. B. Kverno. 1967. Design and analysis of forest-mammal repellent tests. Forest Sci. 13: 333-336.
Hildreth, A. C., and G. B. Brown. 1955. Repellents to protect trees and shrubs from damage by rabbits. U.S. Dep. Agr. Tech. Bull. 1134, 31 p., illus.
Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. (6th ed.) Iowa State Univ. Press, Ames, Iowa. 593 p., illus.

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Experience with Douglas-fir in Southeast Alaska

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) ranges from Mexico to British Columbia and is the most valuable and best-known conifer in the Pacific Northwest. The interior variety, *glauca,* extends northward to latitude 55°N., and the coastal variety, *menziesii,* extends along the mainland to latitude 53°35′N. in the vicinity of Kemano, B.C. Neither variety occurs naturally in Alaska.

Douglas-fir appears to have migrated northward along the coast in British Columbia after the Wisconsin glaciation. Although there is evidence that a refugium existed on Queen Charlotte Islands during the Wisconsin glaciation, pollen records of Douglas-fir have not been found on the island nor from the coastal mainland north of the species' present range. Thus, the present natural range of Douglas-fir appears to represent in a general way its maximum northern extent (Heusser, 1960).

The species grows in a mild and humid region with dry summers. Average annual temperature varies from 45° to 55°F, with an absolute maximum of about 110°F and a minimum of about minus 30°F (Fowells, 1965).

The climate of southeast Alaska appears to be suitable for Douglas-fir growth. It is generally cool and moist with a small range between summer and winter temperature (Andersen, 1955). The maximum recorded at Ketchikan is 96°F; the absolute minimum is minus 8°F, with an average growing season of 170 days. Annual precipitation ranges from 27 inches at Skagway to 248 inches at Little Port Walter on Baranof Island and is well distributed throughout the year.

Experience with Douglas-fir introduced in Alaska shows that the species is able to grow and reproduce beyond its present natural range. Observations from Alaska are only fragmentary and of short duration, but the excellent growth reported here suggests that Douglas-fir may be of future silvicultural value in Alaska.

Experience with Douglas-fir in Alaska

Few attempts have been made to grow Douglas-fir in Alaska. The following five locations are the most significant examples. All are near the southern end of southeast Alaska, from 130 to 220 miles north of the coastal variety's northern natural limit (Fig. 1).

The Hollis Plantation

On May 31, 1952, 12 Douglas-fir seedlings were planted on a recently cutover site near Hollis, Alaska (lat. 55°29′N.; long. 132°40′W.). Seed source was the Cedar River Watershed near Seattle, Washington (lat. 47°25′N.), elevation 1500 ft. By the end of the 1957 growing season eight surviving seedlings were transplanted to a nearby

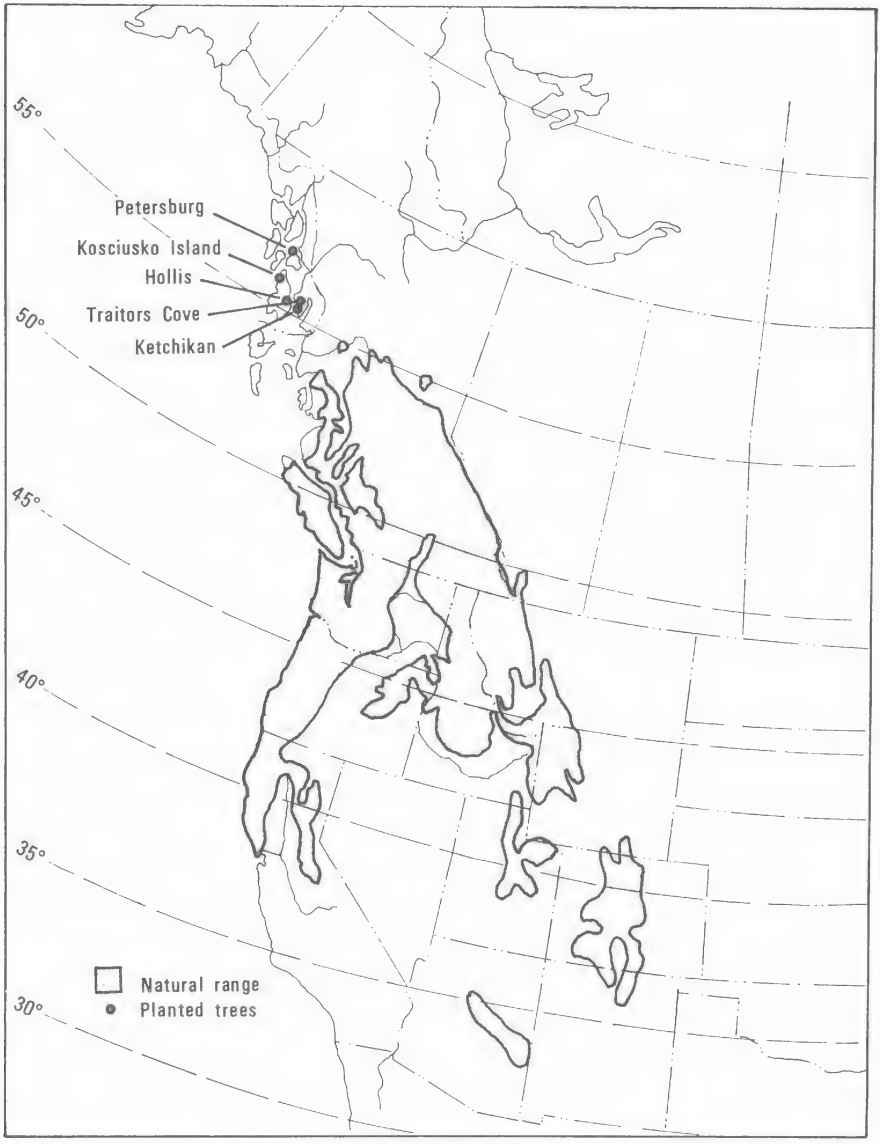

Figure 1. Natural range of Douglas-fir and location of planted trees in southeast Alaska.

south-facing slope in Maybeso Valley, which was clearcut in 1954. The planting site was located near the toe of a slope on deep Karta soil with site index of approximately 150. The site formerly supported a western hemlock-Sitka spruce (*Tsuga heterophylla-Picea sitchensis*) stand and is typical of some of the better sites in southeast Alaska (Gass *et al.*, 1967).

Height growth of the Douglas-fir seedlings was slow before transplanting and remained slow for the first two years after transplanting. Thereafter, growth increased markedly as the root systems became established in their new environment (Fig. 2). By the end of the 1968 growing season, 12 years after transplanting, all eight trees were alive and healthy (Fig. 3). Total heights ranged from 18.3 to 29.5 ft. Average height of the three tallest trees was 28.4 ft, and annual height growth averaged 3.4 ft for the last five growing seasons. This is comparable with growth on a low-site Class II for Douglas-fir in the Pacific Northwest (McArdle and Meyer, 1930). Diameter at

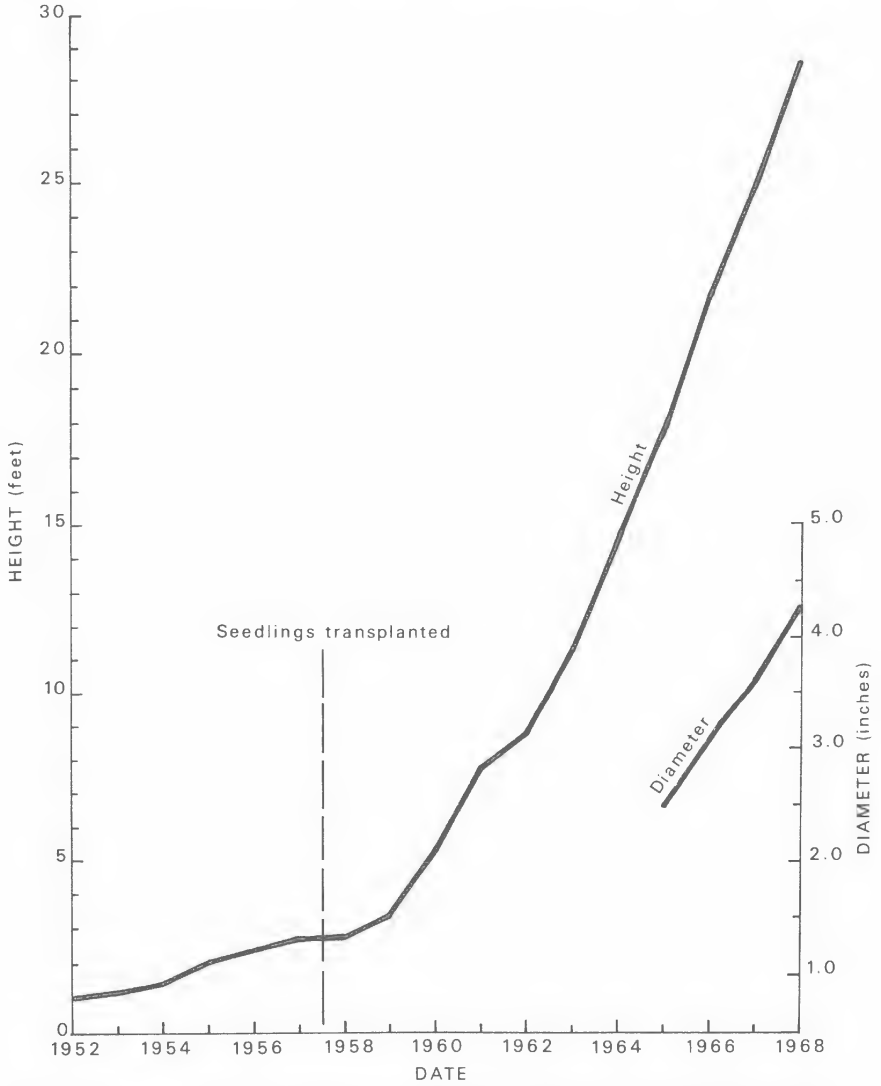

Figure 2. Average height and diameter of three tallest Douglas-fir trees—Hollis plantation.

Figure 3. In 1968 the Douglas-fir trees at Hollis, Prince of Wales Island, ranged in height from 18.3 to 29.5 ft.

breast height has been measured annually since 1965. At the end of the 1968 growing season, average diameter of the three tallest trees was 4.3 inches and diameter growth averaged 0.6 inch per year for the last three growing seasons (Fig. 2).

The trees have shown no sign of frost damage or serious insect damage since planting and have sustained no browse damage, although the area is frequented by Sitka black-tailed deer (*Odocoileus hemionus sitchensis*).

One tree has produced cones for three successive years. In 1966, a heavy seed year for both Sitka spruce and western hemlock, it produced 50 cones. Cones contained seed but a cutting test of 200 seeds showed that the contents of 94 per cent

of the seeds were dried and shrunken, and of 6 per cent were empty. No attempt was made to germinate seed. The following year (1967) the tree produced four cones, and in 1968, 20 cones, but seed was not tested. None of the other Hollis trees have borne cones. The experience of the Hollis plantation shows that Douglas-fir is capable of making excellent growth under forest conditions on a good site in southeast Alaska, at least 130 miles north of its natural range on the coast.

Records of Ornamental Douglas-fir Trees in Alaska

Although the Hollis plantation has produced no viable seed, other Douglas-fir trees planted as ornamentals in southeast Alaska have. In 1966, an exceptionally good seed year, I obtained several dozen cones from two trees located at Mountain Point near Ketchikan (lat. 55°18′N.; long. 131°32′W.), and from one tree in Petersburg (lat. 56°48′N.).[1] The Ketchikan trees were 48 and 38 ft in height and 17.0 and 14.7 inches in diameter in 1967. This height is not indicative of the natural growth rate as both trees were topped about 15 years ago. The Petersburg tree was 35 ft tall and 8 inches in diameter in 1967. All three trees were reportedly over 30 years old, but actual age was not verified. Cones were dried, seed extracted, and 100 seeds from each tree were tested for viability. Unstratified seeds were placed on moist germination pads in petri dishes and maintained between 75° and 80°F with 12-hour daylength for three months. Four seeds germinated from one tree located near Ketchikan, none from the other Ketchikan tree, and nine seeds germinated from the Petersburg tree. All but one seed germinated within five weeks, that one germinating nine weeks after the test began.

The low viability of seed is doubtless due to poor pollination, as only the two trees are known to be growing near Ketchikan and two in Petersburg. However, it is significant that Douglas-fir is capable of producing viable seed as far north as Petersburg, Alaska, 220 miles north of its natural range on the coast.

One additional Douglas-fir tree is located at Traitor's Cove (lat. 55°42′N.; long. 131°39′W.), some 26 miles north of Ketchikan. It is the only known survivor of 70 seedlings planted in 1927, on an area cutover in 1924.[2] The tree is located on a poor site; and although its growth has been only fair, it has competed successfully with natural hemlock and spruce. In 1966 the tree was 8 inches in diameter and 40 ft tall. It is not known whether the tree has ever produced cones.

A Test of Direct Seeding

One attempt has been made to establish Douglas-fir in Alaska by direct seeding.[3] In February 1961, a 10-acre tract of recently cutover land on Kosciusko Island (lat. 56°03′N.; long. 133°33′W.) was aerially seeded with Douglas-fir seed at the rate of 8 oz. per acre. Seed source was Courtenay, B.C., 500- to 1000-ft elevation. Five years after seeding, a search of the area revealed few seedlings. Most of those found were located along a road edge and log landing, where soil was disturbed during log-

[1] I wish to thank Chris Schrader of Mountain Point, Alaska, for permission to measure trees and collect cones, and Ed Browne of Ketchikan for collecting the cones.
[2] Personal communication from R. F. Taylor, Forester-in-Charge (retired), Alaska Forest Research Center, Juneau, Alaska.
[3] U.S. Forest Service Administrative Report on file at the Institute of Northern Forestry, Juneau, Alaska.

ging. The largest seedling found was 18 inches tall and appeared to be healthy. Many seedlings had been browsed by deer.

The seeding was not successful from a silvicultural standpoint, but it shows that, given a suitable seedbed, Douglas-fir is capable of germinating and becoming established from seed, at least 170 miles north of its northern coastal natural limit.

Discussion and Summary

Douglas-fir does not occur naturally in Alaska, and there is no known fossil evidence to show that it has occurred in the state since the Pleistocene. However, under present climatic conditions, the species is capable of germinating, becoming established, making excellent growth, and producing viable seed far north of its present northern coastal natural limit.

Many investigators have concluded that fire is essential for maintenance and spread of Douglas-fir. Judd (1915) recognized that Douglas-fir exists as a temporary forest type which would disappear without periodic forest fires. Munger (1940) presented evidence that, without removal of vegetation by fire or logging, a Douglas-fir forest would be converted to a climax forest type—an uneven-aged stand of hemlock and other shade-tolerant species. Schmidt (1960) concluded, from a review of the species' range in British Columbia, that a denuding factor such as forest fire is necessary for regeneration because insufficient light and unfavorable soil conditions exist beneath a closed forest canopy. He further reasoned that the northward migration of Douglas-fir has been halted by a low fire-hazard barrier.

Schmidt also stated that Douglas-fir is capable of growing successfully in many areas outside its present natural range. As evidence he pointed out that, at its northern coastal limit near Kemano, British Columbia (lat. 53°35′N.), Douglas-fir occurs as high as 2700-ft elevation. Evidence reported here supports Schmidt's statement. Climate apparently does not limit the range of Douglas-fir directly, and so the controlling factor probably lies elsewhere; lack of extensive and repeated fires on the coast north of its present range is a plausible explanation.

It is too early to predict future growth of Douglas-fir in Alaska with certainty. Good performance early in life does not necessarily mean that a species will continue to perform well throughout life. For example, experience with exotics at the Pacific Northwest Forest and Range Experiment Station's Wind River Arboretum in Washington state has shown that many introduced species performed better than native species in early life but were eventually overtaken, mostly before reaching 20 years of age (Silen and Woike, 1959). It is also well known that exotic trees which appear hardy and grow well for many years may be killed as a result of extreme weather conditions. On the other hand, many species, including Douglas-fir, have proved well suited for timber production in Great Britain, where climatic conditions are comparable to southeast Alaska (MacDonald *et al.,* 1957).

A factor in the establishment of Douglas-fir in Alaska is the possibility of introducing with it the Cooley spruce gall aphid (*Adelges cooleyi* (Gillette)). The insect, which has not been reported from Alaska, usually alternates in its life cycle between Douglas-fir and any of several species of spruce (Keen, 1952). It is conspicuous in the coastal areas of Oregon and Washington where Sitka spruce and Douglas-fir coexist but is rarely a serious pest on Sitka spruce except where the tree is planted

outside its natural range. To avoid introduction of the aphid and other pests, future establishment of Douglas-fir in Alaska should be by seed only.[4]

The excellent growth of the Hollis plantation, from a Washington seed source 560 miles to the south, suggests that seed from a variety of sources may be suitable for use in coastal Alaska. It also shows that there may be a place for Douglas-fir in forest management in coastal Alaska when more intensive silviculture is practiced. However, widespread planting should be preceded by test plantings of a collection of provenances or progeny of individual parents. Such care will help in avoiding serious mistakes which could be made in the introduction of a new species.

Literature Cited

Andersen, H. E. 1955. Climate in southeast Alaska in relation to tree growth. U.S. Forest Serv. Alaska Forest Res. Center, Sta. Pap. 3, 11 p.

Fowells, H. A. (Comp.) 1965. Silvics of forest trees of the United States. U.S. Dep. Agr. Handbook 271, 762 p.

Gass, C. R., R. F. Billings, F. R. Stephens, and others. 1967. Soil management report for the Hollis area. U.S. Forest Serv., Tongass National Forest, Alaska Region, 127 pp.

Heusser, C. J. 1960. Late-Pleistocene environments of North Pacific America. 308 p. New York: Amer. Geogr. Soc.

Judd, C. S. 1915. Douglas-fir and fire. Soc. Amer. Forest. Proc. 10: 186-191.

Keen, F. P. 1952. Insect enemies of western forests. U.S. Dep. Agr. Misc. Pub. 273, 280 p.

McArdle, R. E., and W. H. Meyer. 1930. The yield of Douglas-fir in the Pacific Northwest. U.S. Dep. Agr. Tech. Bull. 201, 74 p.

MacDonald, J. A. B., R. F. Wood, M. V. Edward, and J. R. Aldhous. 1957. Exotic forest trees in Great Britain. Great Brit. Forest. Comm. Bull. 30, 167 p.

Munger, T. T. 1940. The cycle from Douglas-fir to hemlock. Ecology 21(4): 451-459.

Schmidt, R. L. 1960. Factors controlling the distribution of Douglas-fir in coastal British Columbia. Quart. J. Forest. 54(2): 156-160.

Silen, R. R., and L. R. Woike. 1959. The Wind River Arboretum from 1912 to 1956. USDA Forest Serv. Pacific Northwest Forest & Range Exp. Sta. Res. Pap. 33, 50 p.

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[4] Personal communication from R. G. Mitchell, Forestry Sciences Laboratory, Pacific Northwest Forest and Range Experiment Station, Corvallis, Oregon.

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Occurrence of Dwarf Mistletoe in Sanitized Ponderosa Pine in South-Central Oregon

Precommercial thinning to increase the productivity of young ponderosa pine (*Pinus ponderosa* Laws.) stands is an accepted practice in the Northwest. The beneficial effects of thinning can be largely negated, however, by the rapid buildup of dwarf mistletoe (*Arceuthobium campylopodum* f. *campylopodum*) in the remaining trees (Fig. 1) unless adequate control measures are taken. Control of dwarf mistletoe in ponderosa pine during precommercial thinning includes cutting visibly infected trees and pruning to sanitize an occasional infected but otherwise desirable tree needed for proper stand spacing.

In some instances, it may be silviculturally desirable and economically sound to prune infected trees as a control measure. However, the biological merits of pruning for dwarf mistletoe control and the occurrence of latent[1] infections in sanitized trees are poorly understood.

This paper reports the occurrence of latent infections over a 10-year period in experimental dwarf mistletoe control plots in south-central Oregon.

Procedure

Data for this report were obtained over 10 years from six 0.05-acre dwarf mistletoe control plots established in 1957 as a part of a larger study. The design of the overall study, methods, and stand characteristics were reported previously (Shea, 1964). In 1957 and before thinning and sanitation, 21 to 77 percent (avg. 47) of the trees on the six plots were visibly infected by dwarf mistletoe.

When plots were established, they were thinned to improve spacing and sanitized by additional cutting and by pruning. Trees with bole infections were removed; trees needed for spacing but with branch infections were pruned following guidelines developed by Shea (1962). Branch infections with the proximal end of the swelling associated with infection over 4 inches from the bole were pruned; those closer were considered bole infections and the tree cut. During the initial plot treatments and the first time thereafter an infected branch was found on a tree, all branches up to

[1] As used here, latent refers to the time between infection and first appearance of aerial shoots.

and two whorls above the infected one were pruned. Subsequent branch infections on trees previously pruned were treated by pruning all branches up to and including the whorl of the infected one.

After plot establishment, the remaining trees were examined yearly to check for newly appearing infection. Infected trees were removed or infected branches pruned before they produced dwarf mistletoe seed. In 1964, the plots were again thinned to reduce stocking to more acceptable levels.

Three of the six plots were within 66 feet of an infected overstory tree which could provide a source of inoculum. To determine if any infections on the study plots resulted from these sources, each newly appearing infection was aged using methods similar to those of Scharpf and Parmeter (1966) for fir dwarf mistletoe. For convenience, the data were converted to an acre basis for computations.

Results and Discussion

In the 1957 reexamination following the initial thinning and pruning, we found and treated an additional 77 bole infections and 1407 branch infections per acre. For the most part, these were small or were swellings without aerial shoots. This result

Figure 1. Ten years after a precommercial thinning without dwarf mistletoe control, infection has increased to damaging proportions in this ponderosa pine.

illustrates the difficulty of finding all infections during the first sanitation and the need for followup examinations. Such missed infections provide a means for rapid proliferation of the parasite soon after sanitation.

Numerous branch infections resulting from new seed were found during the 10-year period on trees in the 33-foot-wide buffer strips surrounding the three plots adjacent to the overstory source of inocula. However, only eight such infections considered established from new seed were found in the plots themselves, and they are not included in our data presentation. All infections on the remaining three plots were judged to have been present when the plots were established.

About 85 to 95 percent of the infections appeared during the first five years after the 1957 sanitation cutting and pruning and 75 to 85 percent within the first three years (Table 1). By 1964, the occurrence of infections had dropped markedly.

TABLE 1. Average annual number of bole and branch infections removed per acre by year after initial plot sanitation.

Year	Infections per acre	
	Bole	Branch
	Number	
1958	23	180
1959	13	103
1960	67	147
1961	13	47
1962	7	110
1963	7	73
1964	3	7
1965	0	7
1966	10	20
1967	13	27
Total	156	721

The increase in bole and branch infections in 1966 and 1967 suggests a possible trend developing for appearance of latent infections. Recent reexaminations show this was not the case. More likely, appearance of latent infections was stimulated by the 1964 thinning which improved conditions for tree growth. Latent infections continued to develop aerial shoots throughout the 10-year period.

The trend for appearance of infections resembles that reported for this dwarf mistletoe in California (Wagener, 1965) and for *A. vaginatum* (Willd.) Presl. in the Southwest (Gill and Hawksworth, 1954; Hawksworth, 1961). Incubation periods following artificial infections usually range from two to six years (Hawksworth, 1961; Scharpf and Parmeter, 1967; Wagener, 1962) with three to four years being most common. Incubation periods up to eight years (Hawksworth, 1961) and possibly for 10 years (Wagener, 1965) have been reported. Thus, dwarf mistletoes can remain quiescent for protracted periods, greatly complicating sanitation and timing of followup cleanings.

Yearly cutting of trees with bole or unprunable branch infections and further thinning in 1964 reduced stocking to 360 trees per acre by 1967. Pruning to remove latent infections from these remaining trees over the 10-year period is summarized in Table 2.

TABLE 2. Leave trees remaining in 1967 and pruned from 1957-67 by number of initial branch infections and times pruned for dwarf mistletoe control.

Initial branch infections	Number of times pruned						Trees per acre
	0	1	2	3	4	5	
			Percent				*Number*
0	46	33	11	10	0	0	160
1	—	40	24	32	4	0	83
2	—	46	35	19	0	0	37
3	—	23	23	44	0	10	30
4	—	54	23	23	0	0	13
5	—	50	50	0	0	0	14
6-10	—	14	30	30	13	13	23

Almost 45 percent of the 360 trees per acre remaining in 1967 had not been visibly infected in 1957; the others had one to 10 branch infections. Of the trees selected initially as mistletoe-free, 46 percent proved to be so; 33 percent required one pruning and 21 percent two to three prunings. Trees initially infected required slightly more pruning than did those initially without visible infections, but 37 percent of all the infected trees required only one pruning. The occurrence of latent infections complicates selection of "uninfected" trees and suggests that pruning, as a control measure, is ineffective in most instances.

Childs (1963) found that the more heavily a tree was infected, the more likely it was to bear latent or overlooked infections. Our data (Table 2) show no such relationship. The absence of such a trend likely results from the extensive pruning infected trees received the first time. Many infections, either latent or missed, were undoubtedly removed when apparently uninfected branches were cut during the first pruning. Thus, there appears to be no conflict between the two data.

Before treatment, the number of infected trees on the plots varied from 21 to 77 percent. We examined the appearance of new infections in relation to these levels by dividing the six plots into two infection classes of three plots each. Those with over 40 percent of the trees initially infected were placed in Class I and those with less in Class II. The two classes averaged 65 and 26 percent infection, respectively. The cumulative total branch infections pruned from each class during the 10-year period are shown in Figure 2.

Marked differences occurred between the total infections developing in the two classes. Those plots with least initial infection had fewer latent infections than did those with greater percentage of trees infected. The initial level of infection appears to be the primary factor determining the amount of subsequent infections developing in infected stands. Childs (1963) noted similar relationships between percentage of trees infected in stands and the number of infections per tree. Means for predicting the relationship between infected trees in a stand and the number of visible and latent infections would be useful in making control decisions for specific areas.

Conclusions

This study brings out several points for consideration by forest managers and suggests areas needing research.

1. Most latent infections produced aerial shoots during the first five years with

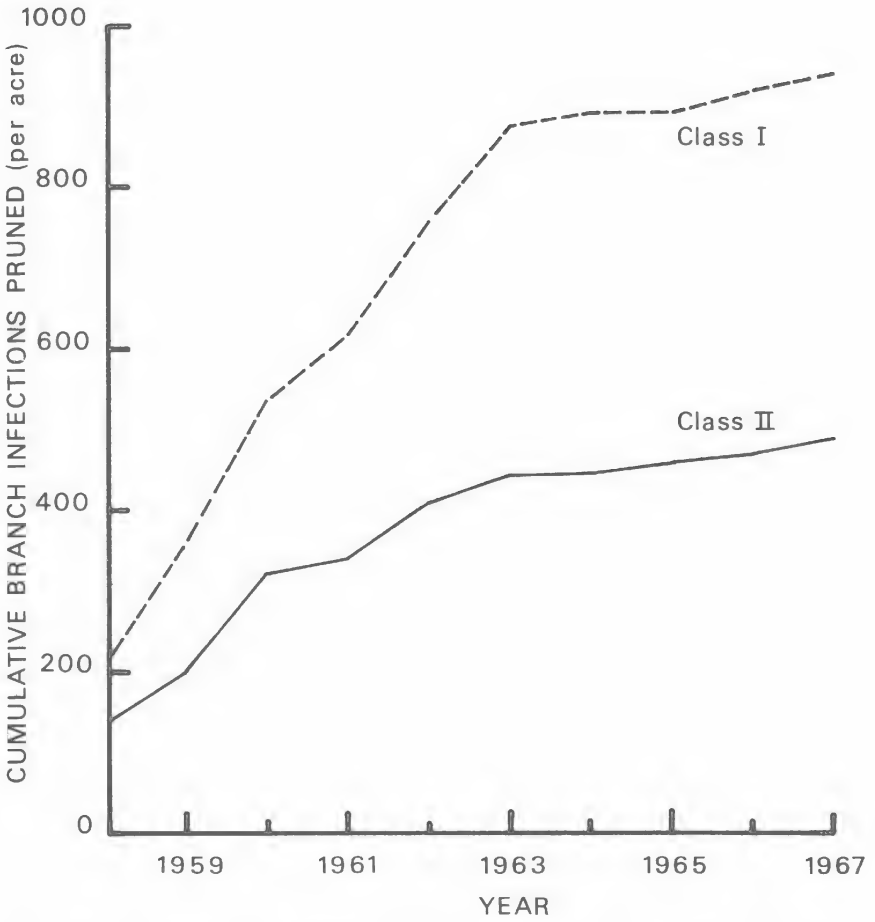

Figure 2. Cumulative number of branch infections per acre pruned yearly by average initial plot infection class and year.

the majority of these occurring during the first three years after thinning and sanitation.

2. Dwarf mistletoe was not eradicated over a period of 10 years, even with yearly sanitations. A control program calling for eradication of dwarf mistletoe by pruning is thus biologically as well as economically unsound.

3. The incidence of latent infections appeared to be positively correlated with initial stand infection levels. Thus, when required, silvicultural control likely will be most successful in stands with very low levels of infection. Additional study is needed so the relationships can be predicted.

4. Knowledge of factors which result in shoot initiation from latent infections could be used to favor or retard shoot production and thus improve the efficiency and timing of sanitation and recleaning.

5. Other control methods may prove useful as adjuncts to cultural ones. For

example, chemical eradicators could reduce the need for repeated sanitations and favor the larger trees which now usually are most severely infected.

6. Pruning to reduce dwarf mistletoe infections is seldom justified in commercial forests. The biological benefits are highly questionable, primarily due to the presence of latent infections in the remaining tree crowns.

Literature Cited

Childs, T. W. 1963. Dwarfmistletoe control opportunities in ponderosa pine reproduction. USDA Forest Service, Pacific Northwest Forest & Range Experiment Station, 19 p.

Gill, L. S., and F. G. Hawksworth. 1954. Dwarfmistletoe control in southwestern ponderosa pine forests under management. J. Forestry 52: 347-353.

Hawksworth, F. G. 1961. Dwarfmistletoe of ponderosa pine in the Southwest. U.S. Dep. Agr. Tech. Bull. 1246, 112 p.

Scharpf, R. F., and J. R. Parmeter, Jr. 1966. Determining the age of dwarfmistletoe infections on red fir. Pacific Southwest Forest & Range Experiment Station, USDA Forest Service. Research Note PSW-105, 5 p.

Scharpf, R. F., and J. R. Parmeter, Jr. 1967. The biology and pathology of dwarfmistletoe (*Arceuthobium campylopodum* f. *abietinum*) parasitizing true firs (*Abies* spp.) in California. U.S. Dep. Agr. Tech. Bull. 1362, 42 p.

Shea, K. R. 1962. The endophytic system of ponderosa pine dwarfmistletoe in relation to swollen branch tissues. Forest Sci. 8: 298-302.

———. 1964. Silvicultural control of ponderosa pine dwarfmistletoe in south-central Oregon—a five-year study. J. Forestry 62: 871-875.

Wagener, W. W. 1962. Dwarfmistletoe incubation period on ponderosa and Jeffrey pines in California. Forest Sci. 8: 16-20.

———. 1965. Dwarfmistletoe removal and reinvasion in Jeffrey and ponderosa pine, northeastern California. Pacific Southwest Forest & Range Experiment Station, USDA Forest Service, Research Note PSW-73, 8 p.

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Influence of Slash Burning on Ion Transport in a Forest Soil

Ion transport in a forest soil is an important part of the mineral cycle of a forest ecosystem. Through this process ions move downward into the soil where they are recycled by the forest, retained within the soil system, or leached from the soil profile. This transport process can be altered by various forest management practices including slash burning, clearcutting, and fertilization. Potentially, slash burning should have the most serious impact on ion transport as it directly affects (1) uptake and return of elements by the forest, (2) the nutrient capital of the soil system, and (3) the mobility of mineral elements within the soil system. In addition to these results the quantities of nutrient ions incorporated in the slash must also be considered since substantial amounts of these nutrients are released to the soil by burning.

Because of difficulties in directly measuring the transport of ions through the soil and lack of sufficient data on nutrient levels in the slash, studies concerning the effects of fire on forest soil have typically considered only the chemical and morphological changes occurring within the profile as determined by sampling before and after burning (Ahlgren and Ahlgren, 1960). Such studies are insensitive to changes in the nutrient status of the ecosystem resulting from slash burning.

This paper reports the results of a pilot study designed to evaluate changes in nutrient release and transfer following slash fires in two different fuel concentrations. A tension lysimeter system was used to examine the relationships of ion release and transfer resulting from burning. This technique permits continuous monitoring of ion concentrations in selected soil horizons. The data thus obtained permit ion transfer within the soil to be evaluated as a function of time. These data in combination with data of nutrient content of the slash material provide information on changes in the nutrient status of the ecosystem following burning.

Methods

The study was conducted at the Allen E. Thompson Research Center (formerly the Cedar River Research Area) located about 35 miles southeast of Seattle in the foothills of the Washington Cascade range. This research center is located in a 40-year-old second-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantation growing on an Everett series gravelly sandy loam, a brown podzolic soil (Typic Haplorthod) derived from Pleistocene glacial outwash. The climate is typical of lower elevations in western Washington, the average temperature in July is 16°C; in January it is 3°C. The average annual precipitation (ca. 144 cm) falls largely during the winter months. The research facilities have been described by Cole (1968). The soils, vegetation, geology, and climate have been described by Cole and Gessel (1968).

During spring 1969, an area about 40 x 70 m was clearcut. This area was adjacent to an existing 0.2 ha clearcut. All logs of small-end diameter greater than 12 cm were removed, and branches and tops were piled for storage. Three plots 1.5 x 2 m each (plots 1 through 3) were established on the clearcut to delineate treatment boundaries. Iron-constantan, three-junction integrating thermopiles were installed in plots 2 and 3 at the surface of the forest floor, at the surface of the mineral soil, and at 2.5, 5, 10, 20, 40, and 80 cm in the soil. Tension lysimeters 620 cm^2 in area (Cole, 1968) were installed in the three plots at the base of the forest floor (or ash layer), at the base of the A-horizon (about 7 cm), at the base of the B-horizon (about 30 cm), and in the C-horizon (1 m). Installation of the forest floor and A-horizon lysimeters in the treatment plots was deferred until after burning to avoid the possibility of heat damage to the acrylic portions of the lysimeters.

Slash composed of needles, branches, and tops was piled evenly on the treatment plots—plot 2 receiving about 7.5 kg/m^2 of slash and plot 3 receiving about 32 kg/m^2 of slash. In addition, forest floor material weighing 1.4 $\pm$ 0.04 kg/m^2 (McColl and Grier, unpublished) was left intact beneath the piles. All weights are on an oven-dry basis at 70°C. The slash piles were then covered with a polyethylene sheet until burning.

Mineral concentration of the fuel load was approximately 0.15 percent nitrogen, 0.11 percent potassium, and 0.16 percent calcium (Cole, Gessel, and Dice, 1967). The forest floor contains 0.86 percent calcium, 0.14 percent magnesium, 0.19 percent potassium, and 0.98 percent nitrogen (Grier and McColl, unpublished). All mineral contents are based on oven-dry weight.

The slash was burned on September 17, 1969. Fuel moisture content then averaged 20 percent of oven-dry weight. Soil temperatures during the fire and for 24 hours after were recorded. The thermopiles were then removed from the soil profile, the vacuum system for the lysimeters installed, and a 0.1 bar tension was established at the lysimeter plates. Plots 2 and 3 were then covered with open-ended polyethylene tents.

To allow examination and comparison of wetting cycles between the treatment plots, they were irrigated every three days (beginning September 28) with uniform water volumes consisting of sprinkled applications of 1.5 cm of water. Eleven days elapsed between burning and the first irrigation. Leachates were collected during the irrigations in separate 100-ml to 200-ml increments. The time required for each sample to accumulate and the sample volume were recorded.

After five irrigations, the treatment plots were uncovered, and weekly bulk collections of solutions from all plots were made. During the irrigation period, precipitation roughly equal to the irrigation fell on the control plot, so total soil solution flow through all plots was about equal. Errors of total ion amount due to different flow rates between the treatment and control plots are small due to the much lower ion concentrations in the control plot solutions.

Measurements of leachate pH, electrical conductivity, and total alkalinity (carbonate plus bicarbonate) were made within 12 hours of collection, using the techniques of Rainwater and Thatcher (1960).

Total dissolved salt content of the solution samples was calculated from electrical conductivity, using an empirical estimation method (Logan, 1961).

Selected samples were digested, using a sulfuric acid and hydrogen peroxide digest,

after which calcium, magnesium, and sodium were determined by atomic absorption spectrophotometry. Organic nitrogen and ammonium in the digest samples were determined by the micro-Kjeldahl method (Jackson, 1958). Phosphorus was determined by colorimetry using the chlorostannous-reduced, molybdophosphoric blue color method of Jackson (1958).

The measured volumes of solutions collected from the different lysimeter plots in the burned plots exhibited higher variability than previously noted at this site (Cole and Machno, in press). This increased variability is partly due to channeling of water by the uneven soil surface and also to water-repellent layers in the upper soil horizons of the burned plots. Because of the high variability, the cumulative leachate flow in Figure 1 and Table 1 was estimated from measurements of water entering the soil. Error introduced by this estimation should be small since evapotranspiration losses at this site are negligible during the cool, wet autumn season.

Results and Discussion

Slash burning substantially alters both the magnitude of ion transport and the proportions of the various ionic species in the soil solution. In this study, the influx of ions to the mineral soil was enormously increased by water leaching through the ash layer (Table 1). Concentrations as high as 80 meq/liter were observed in solutions

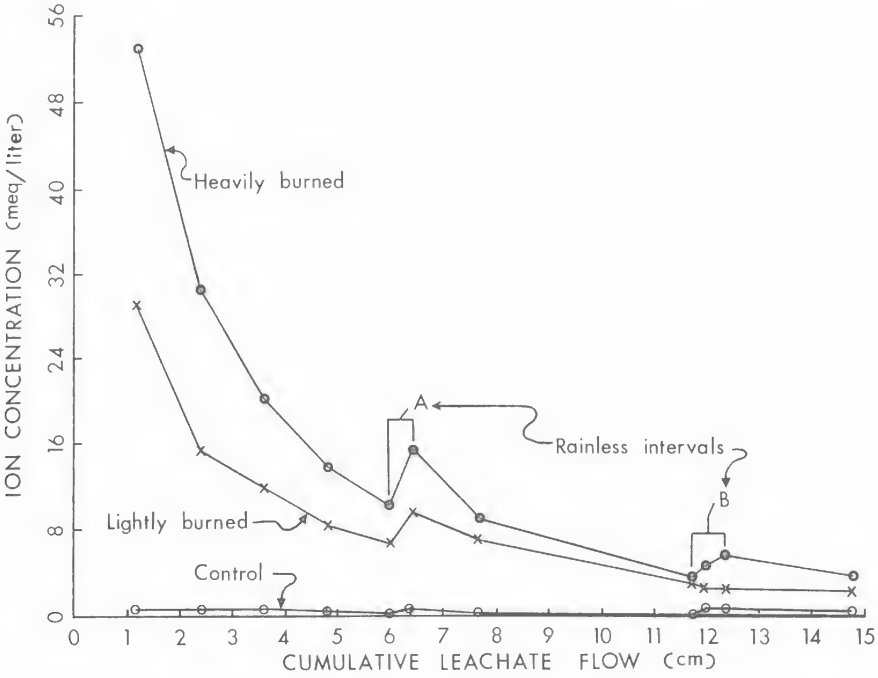

Figure 1. Relationship between cumulative leachate flow (cm) and ion concentration in leachates (meq/liter) from the ash layer or forest floor. The time interval is from 28 September to 23 November 1969. Rainless intervals noted on figure actually represent the first wetting cycle following dry period. Rainless interval A was 14 days, B was two 3-day dry periods with small wetting front between.

entering the soil of the heavily burned plot during the first wetting of the soil after burning. This represents an increase of about 250 percent over concentrations in the control plot. An increase in ion loss through leaching was also noted deep in the soil profile. For example, leaching losses from the 1-m soil depth increased 3.3 times on the lightly burned plot and 4.5 times on the heavily burned plot over leaching losses from the control plot (Table 1).

TABLE 1. Total ion amount collected from soil horizons subjected to various treatments from 25 September to 23 November 1969.

Horizon	Total ion (meq)*		
	Control	Light burn	Heavy burn
Forest floor**	5.3	76.9	128.0
A-horizon	5.6	85.1	78.8
B-horizon	2.1	7.2	16.2
C-horizon	2.4	7.8	11.4

* Total ion estimated on basis of uniform flow through soil and measured ion concentrations.
** Forest floor or ash layer.

Leaching of the soluble ash constituents from the ash layer was the major contributor of ions to the soil solution. There was little if any addition of ions to the leachates as they passed through the heated portion of the mineral soil. This result could be expected since heat flux from the fire did not substantially increase the temperature of the underlying mineral soil. The maximum surface temperatures were about 410°C on both plots, while at the 2.5-cm soil depth the maximum temperatures were 41°C on the lightly burned and 84°C on the heavily burned treatment plots. Soil moisture in the upper 10 cm of soil ranged between 10 and 30 percent before the fire. Higher or lower soil moisture could produce different results by changing the thermal conductivity of the soil.

The mineral soil played an important role in regulating the downward movement of ions released by the ash layer. The A- and B-horizons adsorbed 70 to 90 percent of the ions entering the soil from the ash layer (Table 1). In the two months under discussion, the A- and B-horizons of the lightly and heavily burned plots adsorbed about 1.1 equiv/m^2 and 1.8 equiv/m^2, respectively, from the soil solution.

The ion concentration of the solution that was leached from the ash layer decreased rapidly as a function of total flow (Fig. 1), indicating that much of the ash was readily soluble and rapidly depleted. However, the ion concentrations of the ash leachates remained above those of the forest floor leachates from the control plot throughout the period reported, indicating the presence of less soluble ash components. This finding suggests a differential release of ions from the ash layer, the more soluble constituents comprising a major portion of the ion content of the early wetting cycles.

Two environmental factors also appeared to influence the ion concentration of the soil solution, these being soil solution flow rates and the length of time between wetting cycles. The flow rate of the soil solution, which in this well-drained soil is governed by precipitation rate, was inversely related to ion concentration (Fig. 2). The inverse relationship suggests that chemical equilibrium between soil and solution was not achieved in the soil system under conditions of high flow.

The time elapsed between wetting cycles also influenced ion concentration in the soil solution. Figure 1 shows that increases in ion concentration coincident with rainless periods occurred between 6 and 7 cm of total flow and again between 11 and 13

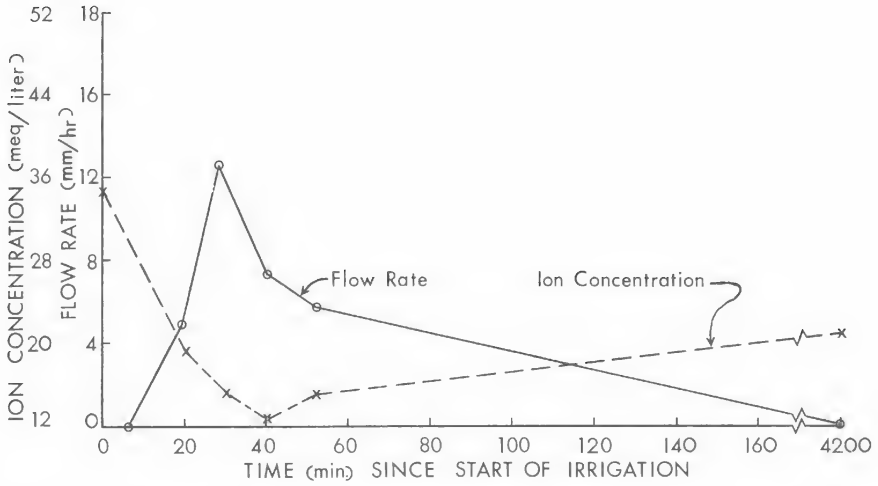

Figure 2. Ion concentration and flow rate of leachates from the A-horizon of the lightly burned plot as a function of time elapsed since the beginning of irrigation.

cm of total flow. This phenomenon was also noted by McColl (1969) in an undisturbed Douglas-fir ecosystem at this research site. He found that the length of the period preceding the wetting front was a major component increasing the ion concentration in the soil solution, and he also found an inverse relationship between flow rate and ion concentration in the soil solution.

In addition to changing the total ion concentration of the soil solution, burning also altered the concentration and proportion of various ions in the soil solution (Table 2). Potassium, for example, was present in the forest floor leachates from the control plot on September 28 at 0.1 meq/liter, or about 30 percent of the total cations. In the leachates from the burned plots of the same date, potassium comprised 60 to 80 percent of the total cations and was present in concentrations as high as 25.3 meq/liter. Only trace amounts of potassium were lost from the rooting zone, however. Magnesium, on the other hand, comprised only 15 to 20 percent of the cations entering the soil from the ash, but comprised as much as 50 to 60 percent of the cations lost from the rooting zone. Calcium was the major cation in the unburned fuel (Cole, Gessel, and Dice, 1967) and presumably also in the ash, but it was only a minor constituent of the soil solution from the burned plots (Table 2). The small amount of calcium in the soil solution can probably be explained by the physical-chemical behavior of calcium salts in high pH ranges.

The bicarbonate ion was the major anion in the leachates from the treatment and control plots. The carbonate ion was also present in the initial leachate collections from the surface horizons of the treatment plots, but in all cases was less than 10 percent of the total anions. Phosphate concentrations were highest in the leachates of the lightly burned treatment plot and lowest in the heavily burned treatment. Although reported as PO_4^{3-} in Table 2, the $H_2PO_4^-$ and HPO_4^{2-} forms are probably dominant in the solutions. This conclusion could explain part of the discrepancy between calculated total ion and the analytical total in the control plot leachates. Qualitative tests

TABLE 2. Ion concentration (meq/liter) of soil solution from different soil horizons for wetting cycles on 28 September (I) and 23 November 1969 (II).

Treatment	Horizon*	Total ion (calculated)		Ca^{2+}		Mg^{2+}		K^{+}		Na^{+}		pH		Alkalinity (total)		$(PO_4)^{3-}$	
		I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Control	F	0.28	0.28	0.09	0.16	0.10	0.13	0.10	T	0.01	0.04	6.2	6.0	0.18	0.16	0.92	0.03
	A	0.27	0.27	0.05	0.08	0.14	0.10	0.12	T	0.01	0.06	6.2	6.7	0.17	0.14	0.35	T
	B	**	0.19	**	0.07	**	0.07	**	T	**	0.05	**	6.4	**	0.14	0.23	T
	C	**	0.23	**	0.10	**	0.10	**	T	**	0.04	**	6.7	**	0.20	0.17	T
Lightly burned	F	17.10	2.52	0.09	0.02	1.08	0.36	13.65	1.60	0.41	0.04	8.1	7.6	5.89	1.42	1.34	0.01
	A	18.70	2.42	0.07	0.03	1.70	0.77	13.06	1.10	0.49	0.04	7.9	7.4	6.05	1.76	1.15	0.01
	B	**	0.37	**	0.01	**	0.18	**	T	**	0.02	**	6.6	**	0.14	**	T
	C	**	0.52	**	0.01	**	0.32	**	T	**	0.04	**	7.0	**	0.40	**	T
Heavily burned	F	34.10	4.00	0.17	0.08	7.24	3.13	25.29	1.80	1.02	0.12	8.9	8.1	14.16	3.60	0.59	0.01
	A	19.70	2.63	0.14	0.03	3.34	0.70	12.17	1.40	0.57	0.06	8.0	7.7	9.83	1.76	0.48	0.01
	B	**	1.47	**	0.03	**	0.82	**	T	**	0.08	**	7.2	**	0.72	**	T
	C	**	0.97	**	0.03	**	0.64	**	T	**	0.06	**	6.8	**	0.70	**	T

T<0.01 meq/liter.
*F=forest floor or ash layer.
A=A-horizon (7 cm).
B=B-horizon (30 cm).
C=C-horizon (1 m).
**Wetting front had not reached these depths on 28 September 1969.

showed that substantial amounts of sulfate and silicate were present in the solutions from the treatment plots, but tests for nitrate and chloride were negative.

Organic nitrogen and ammonium nitrogen were present only in trace amounts in the soil solution of the treatment plots. Tests for nitrate were negative, so it is concluded that little nitrogen was released to the soil solution as a result of burning.

Conclusions

Slash burning produced the following changes in the ion regime of this soil.

1. Burning caused substantial increases in the concentrations of ions entering the soil. Ion loss from the rooting zone also increased. These increases are related to the weight of fuel on the soil surface.

2. Leaching of ions from the ash layer caused the major chemical changes occurring in the soil. There was no evidence that heating of the mineral soil appreciably affected the chemical composition of the leachates.

3. Most of the ions leached from the ash layer were adsorbed in the A- and B-horizons of this soil.

4. Total flow, flow rate, and time between wetting fronts influence the amount of ion transport after burning.

5. The principal anion in the soil solution of the treatment plots was bicarbonate, but carbonate, sulfate, phosphate, and silicate were also present. Leaching loss of nitrogen occurred only in trace amounts and at concentrations less than in the control plot.

6. Calcium was the major cation in the fuel while potassium was the major cation leached from the ash layer, and magnesium was the major cation leached from the rooting zone.

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Literature Cited

Ahlgren, I. F., and C. E. Ahlgren. 1960. Ecological effects of forest fires. Bot. Rev. 26: 483-533.

Cole, D. W. 1968. A system for measuring conductivity and rate of flow in a forest soil. Water Resour. Res. 4: 1127-1136.

————, and S. P. Gessel. 1968. Cedar River research—a program for studying the pathways, rates and processes of elemental cycling in a forest ecosystem. Forest Resour. Monogr. Contrib. No. 4. Univ. of Wash., Seattle. 53 pp.

————, Gessel, S. P., and S. F. Dice. 1967. Distribution and cycling of nitrogen, phosphorus, potassium and calcium in a second-growth Douglas-fir ecosystem, Pp. 197-232. Symp. Primary Productivity and Mineral Cycling in Natural Ecosystems. Ecol. Soc. Amer., AAAS Annual Meeting, Dec. 27, 1967. New York.

————, and P. Machno. In press. Factors affecting percolation in forest soils. Proc. Symp. Water Balance in North America. Amer. Water Resour. Assoc. June 23-26, 1969. Banff, Alberta.

Jackson, M. L. 1958. Soil Chemical Analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J. 498 pp.

Logan, J. 1961. Estimation of electrical conductivity from chemical analysis of natural waters. J. Geophys. Res. 66: 2479-2483.

McColl, J. G. 1969. Ion transport in a forest soil: models and mechanisms. Ph.D. Thesis, Univ. of Wash., Seattle. 214 pp.

Rainwater, F. H., and L. L. Thatcher. 1960. Methods for collection and analyses of water samples. U.S. Geol. Surv. Water Supply Paper 1454. 301 pp.

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The Ecology, Distribution, and Taxonomy of the Millipeds of Montana West of the Continental Divide

Introduction

The present study began as the first attempt, in this country at least, to investigate the ecology of an entire milliped fauna in a relatively large area of mountainous country. When collecting disclosed the fact that 22 species and one variety were represented in the area, and that over half of them had never been described, the report was expanded to include the taxonomic aspects of the fauna as well. Unquestionably, the most noteworthy feature of these new species was that 10 of them belong in the order Chordeumida, a proportion far exceeding that of other large areas elsewhere in the United States.

The study is based upon two collections of millipeds, one made during 1956 and earlier years by Royal Bruce Brunson and some of his students. Records from this collection are designated by the prefix D. When no collector's name is given, the collector was Royal Bruce Brunson. The second collection was made by Rupert Schmitt with help from Richard H. Russell and other friends. The collecting occurred primarily in the summer during 1964, 1965, and 1966. These records are designated by the prefix M. When no collector's name is given, the collector was Rupert Schmitt. Collecting trips were made two or more times to each county in Montana W of the Continental Divide. Most of the millipeds were discovered by rolling over rocks, logs, and other covering materials, and examining carefully the newly exposed area for specimens. Usually they were picked up with a BB forcep, or fingers, and placed in a vial containing a solution of one part glycerine to 10 parts of 70 percent ethyl alcohol. Habitat information recorded included the microhabitat and local vegetation. Any salamanders recorded were identified by Ken Teberg. An altimeter was used to record some of the elevations, and other elevations were taken from Forest Service maps. The elevations given in this paper are all approximate. Usually when a site was collected, all of the specimens at that site were placed in a single vial, to save vials and the time of writing duplicate labels. In addition, some of the species were difficult to separate in the field because of their close resemblance to each other and differences could often be determined only by laboratory study, involving searches of literature, and dissections of the male reproductive organs, the gonopods, which are a major indicator of species in the millipeds. This lack of separation of species in the field has undoubtedly allowed a few errors to slip into the information on the microenvironments.

Areas collected included flood plains, the bases of talus slides, the borders of small creeks in canyons and ravines, and areas high in the mountains such as lakes and passes. Most areas were within a short distance of the automobile, but others were reached by back-packing into the mountains. In a majority of the localities where a search was conducted, no millipeds were found. The absence of records for some areas often indicated an unsuccessful hunt. This result was especially true in the more xeric southern part of the region. However, counties which were more productive of millipeds were collected more intensively.

In Montana, W of the Continental Divide, rainfall is lowest in the SE. This area includes Deer Lodge and Silver Bow counties, where, despite two collecting trips, no millipeds were discovered. More searches should be made of this area. A low population may merely indicate the effect of low rainfall in the area. If no millipeds occur in the area, the cause may be environmental pollution. The mining and refining of copper and other metals occur in those two counties. The fumes and fallout from these operations may be toxic to millipeds. By their absence, millipeds may be valuable indicators of environmental pollution. The northern counties were also collected twice, and produced few millipeds. Much of the northern area seemed to possess vegetation more characteristic of drier regions with lesser rainfall than the precipitation maps would indicate. By contrast, the W side of the Mission Mountains had vegetation which seemed more characteristic of heavy rainfall than the precipitation map of the U.S. Department of Agriculture would indicate (U.S. Dept. of Agric. 1941). A difficulty in obtaining reliable precipitation data for the mountain slopes results from the fact that many of the stations recording precipitation are located in the cities which are located in the valleys and not on the slopes of the mountains. The mountains have a much larger area, with large differences in precipitation due to elevation and exposure, and have higher rainfall on most slopes than in the nearby valleys.

Soil Moisture: Requirements

Several species of millipeds were collected on ecounits of the Lubrecht Experimental Forest of the Montana Forest and Conservation Experiment Station. The station conducted research in which seven ecounits were established on a gradient ranging from xeric to mesic. Each of them was equipped with stacks of fiberglass units to measure soil moisture and temperature. The moisture content of the soil was graphed showing the percent of moisture of the weight of the soil. An ecounit was defined as a plot of uniform land form and relatively uniform flora (Blake *et al.,* 1965; Nimlos *et al.,* 1963 or 1964).

Following are a numbered list of the ecounits, some of their major characteristics, and the species of millipeds collected at each ecounit. Information on the vegetation and soils is in the study plans and progress report (Nimlos *et al.,* 1963 or 1964) Ecounit 1: the driest site, located on a steep, south-facing slope and having shallow soil, only 12″ deep above bedrock. On July 15, 1963, the soil moisture at a 3″ depth was 10% and at a 12″ depth 13%. On Dec. 19, 1962, before the ground froze, the figures were 27% moisture at 3″ and above 29% at the 12″ depth. About 50′ down the slope from the measuring equipment, many *Bollmaniulus montanae* chamberlin were collected on Aug. 4, 1964, from beneath ponderosa pine needles which were

dry on top and damp by the ground (from a rain the previous day). The millipeds were slow or motionless when uncovered and underneath them was ½″ to 1″ of dry duff, and under the duff powdery dry soil. Below the slope, the ground was more level, and *B. montanae* and *Aigon parvior* were collected under boards and a piece of steel roofing on Aug. 4, 1964. Ecounit 1½ faced S and was dry. *B. montanae* was collected from underneath a rotten log, July 22, 1965, the day after rain. Ecounit 2 faced S and was dry. On Aug. 3, 1965, *Brunsonia complexipes* was in humus in a depression by a log near many deciduous shrubs and herbs on a day with occasional rain, after a dry spell. On July 15, 1963, the soil moisture was 37% at a depth of 3″ and 51% at a depth of 42″. Ecounit 3 was characterized as being slightly moist. *Brunsonia complexipes* was in humus in a depression left by an uprooted tree at the edge of the forest, Aug. 3, 1965. On July 15, 1963, the soil moisture was 10.5% at a depth of 3″ and 34% at a depth of 42″. Ecounit 4 was called moist and had a N aspect. *Brunsonia complexipes* was collected under a rotten log, July 22, 1965. Ecounit 5 was wet, and had much moss and downed timber. On Aug. 4, 1965, immature Conotylidae were collected. On July 15, 1963, the soil moisture was 45% at a depth of 3″ and 19% at a depth of 42″. Ecounit 6 was characterized as being very wet, and on July 22, 1965, many *Endopus parvipes* were in leaf litter. On July 15, 1963 the soil moisture was estimated at 60% at 3″ and 25% at a depth of 42″.

This moisture information indicates that the *B. montanae* can probably tolerate and survive at soil moistures of under 13% (unfortunately we have no figures available for two of the driest months, Aug. and Sept.). Members of the Conotylidae occurred in environments which had much more available moisture. Perhaps *Endopus parvipes* requires more moisture than *Brunsonia complexipes*. It would leave a false impression on the reader, if we would try to state exactly the moisture requirements of these millipeds until such time as the collecting could be correlated closely with moisture records taken on the same day.

Many species were collected within 4 miles of Noxon, in an area of heavy rainfall. Noxon area species include: *Chonaphe serratus, Isaphe convexa, Montaphe elrodi, Orophe cabinetus, Ectopodesmus cristatus, Kepolydesmus anderisus, Bollmaniulus montanae, Mimolene sectile, Brunsonia complexipes, Corypus cochlearis, Striaria* sp., and *Orthogmus oculatus*. This is an area with magnificent forests of red cedar, Douglas-fir, and *Larix*. Thick humus covers the forest floor. The collecting was done at lower elevations.

The Distribution and Evolution of Montana Millipeds

Some of the factors which influence plant distribution also affect milliped distribution. Habeck (1967) wrote that he suspected that the range of Pacific coast floristic elements was formerly much greater. Easternmost populations of *Tsuga mertensiana, Thuja plicata, Tsuga heterophylla, Abies grandis,* and *Taxus brevifolia* occur now "as small, disjunct, relict populations, some distance from areas where these species show general widespread distributions." He felt that macroclimatic changes were responsible for a withdrawal of the Pacific coast floristic peninsula from Montana.

The millipeds and other land invertebrates, which are closely tied to particular moisture requirements, are also affected by the macroclimate. As the climate became drier, it would be expected that their populations would also change. A single pop-

ulation occupying a continuous area would become split up into many populations. If these populations were isolated from each other long enough, each of them might have a tendency to adapt to local conditions and eventually might develop into new species and new genera. The large number of species endemic to Montana and the Northern Rocky Mountain region seems to indicate that this has occurred. Speciation could be expected to occur rapidly in the millipeds because of the short life cycle and their dependency upon a humid microclimate. The inability of most of them to tolerate xeric conditions for very long isolates them and restricts their freedom of movement. It would be expected that large migratory movements could enable populations to mingle and perhaps interbreed. However, any migratory activity would have to occur during rainy periods, when sufficient moisture would be available to maintain life and when the temperature would not restrict movement by being too cold or too hot. In referring to the millipeds, Loomis (1938) stated "by far the largest number of species are definitely humus inhabitants, delicate creatures, most of them unable to withstand a few moments of hot sunshine or somewhat longer exposure to extreme dryness, whether above or below ground." Cloudsley-Thompson (1962) stated that "humidity is the most important climatic factor affecting the distribution of woodlice, millipeds, centipeds, and other arthropods that lack an efficient water-proofing mechanism. These animals are of necessity cryptozoic and generally only emerge from their daytime retreats when the temperature drops and the relative humidity of the atmosphere increases." An exception to this behavioral pattern occurs with millipeds when drought occurs, at which time mass migrations have taken place as the animals seek moisture (Cloudsley-Thompson, 1963). An additional factor affecting milliped movement is a tendency they have to avoid the light (Cloudsley-Thompson, 1958).

Further study will probably disclose much variation between the individual isolated populations of some of the Montana species. The barriers often causing the isolation of the Montana species are many. A population living in a ravine will be isolated altitudinally by conditions existing at the higher elevations which cause much dryness from the sun and wind in summer, and other barriers in the form of a long retention of the snow cover of winter. Habeck wrote of the effect of climate on this zone for plants. The climate is more harsh to living things above timberline. This upper limit to tree growth is effected by macroclimatic changes and retreats or advances occur in response to major climatic changes. Sometimes the timberline zone is very unstable as at Logan Pass in Glacier National Park (Habeck, 1969). If a dense forest were to develop at the higher elevations, it could provide a corridor for millipeds to travel from one side of a mountain range to the other. In our study, chordeumid millipeds were observed in such forested areas covering mountain passes. However, the other orders of millipeds were not collected in the areas close to mountain passes, but were at lower elevations. For them the higher elevations seemed to form an effective barrier. At the lower elevations a population may encounter obstacles in the form of rivers, or periodically flooded flood plains. A study by Dowdy shows high populations of millipeds on a flood plain in Missouri. However, he collected only 5 species on the flood plain, as contrasted with 14 species in an oak hickory community. The covering of a flood plain with water, however, apparently completely eliminated the millipeds from the flood plain (Dowdy, 1968). During our research, few millipeds were collected from flood-plain areas. For Mon-

tana, at least in 1965-1966, flood plains were a poor habitat. Few millipeds were collected in grasslands. The clearing of land for grazing has created another barrier. The land becomes exposed to the sun and wind because of removal of much of the humus and shading vegetation, other than grass. The ridges, which isolate one creek from another, also form a barrier because they are much more xeric in nature than the shaded low places along streams where moisture frequently remains for long periods of time and where the vegetation is different, often having more broad-leaved plants than the ridges which have a much higher percentage of coniferous plants.

The studies on which this paper was based resulted from much more intensive collecting than is known to have been made in any other areas of like size in the Western states. It is thought that all features of the milliped fauna of western Montana now are remarkably well known. The four species previously reported from the state have been found; five other recognized species were added to the fauna; and 13 new species with one new variety were discovered. Thus, 22 species and a variety now constitute Montana's milliped fauna.

Disposition of specimens from this study is as follows: the holotype and a paratype specimen (where present) have been deposited in the Myriapod Collection of the U.S. National Museum; other specimens have been sent to the following depositories: University of Montana, Invertebrate Collection, Missoula; Dr. Howard V. Weems, Jr., Florida State Collection of Arthropods, Div. of Plant Industry, Dept. of Agriculture, Gainesville, Fla.; some specimens have been retained by Rupert Schmitt, Skagit Valley College, Mount Vernon, Washington.

Polyxenida: Polyxenidae

Polyxenus lagurus (Linnaeus)[1]

Range and Habitat Records: Several specimens 100 ft from Clark Fork River, under rocks on well-drained hillside, Missoula, Missoula Co., Apr. 15, 1965, M-6521. Many specimens under rocks on boards, Nimrod (Burn Resort), Granite Co., Apr. 28, 1965, M-6522, R. H. Russell collector.

Remarks: *Polyxenus lagurus* occurs throughout Europe, and also has been collected in Nova Scotia. Some of the records for *P. fasciculatus* probably pertain to *P. lagurus* (Chamberlin and Hoffman, 1958). In Europe *P. lagurus* is often myrmecophilous (Donisthorpe, 1927). The closely related *P. fasciculatus* is "found along the Atlantic coast under the bark of trees and under stones," and lives "on plant and animal waste, possibly also on plant lice, in which case they are of economic value" (Williams and Hefner, 1928). One reason for the paucity of records in the U.S. is the diminutive size of *P. lagurus,* for to the naked eye it appears more like a light-colored piece of lint, or a speck of debris instead of a beautiful tiny milliped complete with a fringe of microscopic hairs.

Polydesmida: Eurydesmidae

The Montana species of this family all occur in forests which receive heavy rainfall or have extensive moisture in the local area. Often they occur in areas with heavy humus, and nearby vegetation characteristic of the Pacific coast forest with trees such as red cedar and Douglas-fir.

Chonaphe serratus, new species

Many specimens, including male helotype, mating under rocks along road, 1 mi W of Noxon, near graveyard, T26N, R33W, S17, Sanders Co., May 2, 1965, M-657. Other specimens also from Sanders Co.: large group crawling on damp earth on bright sunny morning, 1 mi W of Noxon, near graveyard, T26N, R33W, S17, June 17, 1966, M-6568; under logs and in rotten wood, Bull River campground, 4 mi NW of Noxon, T26N, R33W, S3, May 2, 1965, M-656; female under moss at base of talus slide, Bohanan Creek, 2 mi N of Yellow Bay, Lake Co., July 23, 1965, M-6537, Ken Teberg.

Diagnosis: Since only about 30 mi separates the type locality of *C. patriotica* from that of *serratus*, it is quite likely that the latter species will be found merging with the former, but on the basis of the illustrations and very meager description of *patriotica,* two species, at present,

[1] For synonymy of this genus and species see Chamberlin and Hoffman, 1958.

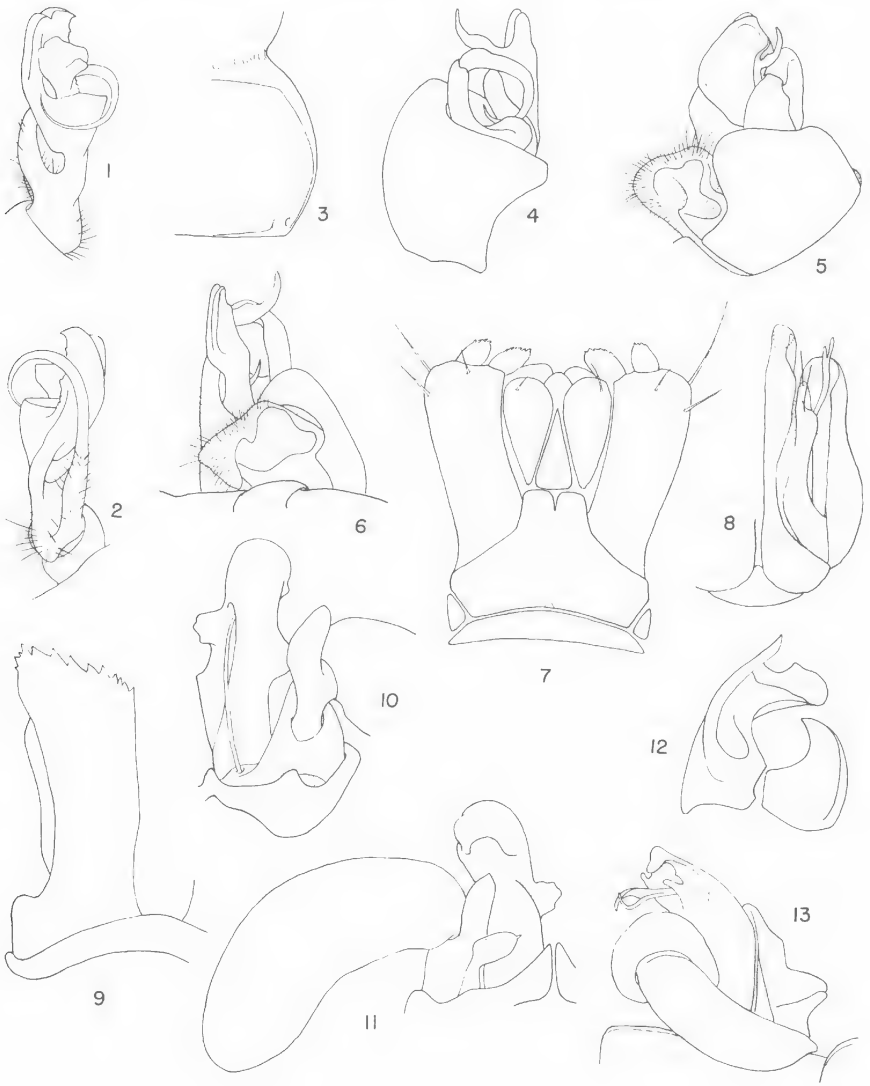
appear to be represented, separated by differences of the gonopods and possibly body size.

Description: 29-32 mm, width 5-5.7 mm; color as in *patriotica.* Males slightly less convex than females. Lateral keels strongly produced backward on segments 17-19, only those of 19, at most subacute. Second joint of legs from middle of body caudad ending in a small ventral spine, largest on segments 14, or 15 to 16.

Gonopods as shown in Figures 1 and 2; the heavy distal branch subdentate to dentate along mesal margin; median process much flattened, not chalice-like as shown in illustration for *patriotica;* subbasal process forming a pocket in which the outer portion of the slender basal branch usually is coiled.

Margin of gonopodial opening at level of metazonite in front but rising rapidly from sides and very high behind the gonopods, the opening deeply emarginate.

Third sternum in both sexes very narrow, with 2 small conic tubercles; fourth sternum wider, with 2 larger, more broadly conic tubercles in male but lacking in female; fifth male sternum



rapidly descending, that of female higher. Segment 6 with both sterna deeply depressed in male to level of metazonite.

Ecology: This species was collected only in the Noxon area, which has dense forests of red cedar, and Douglas-fir, and the forest floor is covered with deep humus. A member of the same genus, *Chonaphe armatus* Harger, occurs widely in the Puget Sound region of Washington and probably occupies habitats similar to that of *C. serratus* (Hannum, 1926).

Isaphe convexa Cook 1904

Three males, 2 females, under rocks in rock slide, W side of river, 3 mi N of Thompson Falls, Sanders Co., T22N, R30W, S36, May 1, 1965, M-655; 5 males, 1 female, many young, under and in rotting logs, Bull River campground, 4 mi NW of Noxon, Sanders Co., T26N, R33W, S3, May 2, 1965, M-656; female, Bobcat Creek, near entrance to Rock Creek, Granite Co., June 20, 1965, M-6511; female, just out of splash, Skalkaho Falls, Ravalli Co., Highway 38, June 18, 1966, M-6578; female, shore, Pend O'Reille Lake, East Hope, Idaho, June 17, 1966, M-6577; Lincoln Co., under cedar bark along Giant Cedar Trail, Ross Lake Creek Scenic Area near Bull Lake, Aug. 10, 1965, M-6564; Lake Co., under moss on a stabilized area at base of talus slide, 2 mi N of Yellow Bay, July 23, 1965, M-6537. Previously known only from the type locality, Kootenai Co., Idaho, which is close to Sanders Co., Montana.

In general agreeing with the original description and illustrations except that the first segment measures approximately 1.5 mm long and 5 mm wide, thus being shorter than stated. The gonopods have conspicuously fewer bristles than shown in the illustrations.

Ecology: Collected from only four localities, but from three counties. In two locations they were associated with rock slides, and in the other two locations they were collected from beneath plant material on the forest floor.

Montaphe elrodi Chamberlin[2]

Three males, 4 females, mating under rocks along road, 1 mi W of Noxon, near graveyard, T26N, R33W, S17, Sanders Co., May 2, 1965, M-657.

In these specimens the vertex of head is smooth and shining, not at all coriaceous; the lateral limits of segment 1 extend slightly below those of segment 2; and the metazonites lack a distinct transverse furrow although being very faintly depressed. The gonopods, however, do not show any striking differences that might be considered as indicating a different species.

Ecology: Specimens were obtained from the following microenvironments (with number given of collections from each environment): Between rocks (1), under rocks (3) (some of the rocks moss-covered), under moss (1), under logs (2), under bark (2), and in rotten wood (2). It appears that *M. elrodi* seeks refuge beneath a wide range of objects, and shows no strong preference for the type of covering. Many of these sites were mossy, and were located in well-forested areas having vegetation characteristic of areas with much moisture or precipitation. Two groups were observed on top of wet moss, in one of these groups copulation was observed, on June 26, 1965, after rain had fallen the previous night. A common location was in creek bottoms having a thick layer of humus and red cedar, maple, cow parsnips, and other vegetation of moist areas. A few creek-bottom areas had more xeric vegetation nearby such as ponderosa pines. Elevations ranged as high as 6000 ft, but most specimens were collected at elevations under 4500 ft. All of the Montana specimens were found in the more southerly part of the watershed, or along the Bitterroot or Blackfoot branches. This distribution pattern may reflect the lower precipitation and drier forests of the areas South and East. A large population is in the central part of western Montana, with many occurring on the western slopes of the Mission Mountains. This is an area of dense forests often composed of red cedar along the creeks and moist lower slopes of canyons. No *M. elrodi*, however, were collected in the cedar grove near the Avalanche campground in Glacier National Park. It is possible that any population which might live in that area was hard hit by heavy rains and a flood, a few years prior to this study. Perhaps future collections will extend the range northwards into that area.

Other Distribution and Habitat Records: Lake Co.: Common in this county where it was found in 21 different locations: at an elevation of 6000 ft under a rock along the North Crow Creek in a partly open area of alpine firs, spruce, cow parsnips, yellow violets, and moss, July

[2] *Ibid.*

Figures 1-2, *Chonaphe serratus.* 1, left gonopod, anterior view; 2, same, posterior view.

Figures 3-6, *Ectopodesmus cristatus.* 3, keel, male segment 9; 4, left gonopod, anterior view; 5, same, oblique lateral view; 6, same, posterior view.

Figures 7-8, *Mimolene sectilis.* 7, female gnathochilarium; 8, right gonopod, anterior view.

Figures 9-11, *Adrityla cucullata.* 9, left anterior gonopod and sternum, anterior view; 10, right posterior gonopod, anterior view; 11, same, posterior view.

Figure 12, *Austrotyla montani.* Left anterior gonopod and coxal joint of posterior gonopod, mesal view.

Figures 13-15, *Brunsonia complexipes.* 13, both left gonopods, lateral view; 14, coxal, second, and base of outer joint of left posterior gonopod, posterior view; 15, left anterior gonopod and sterna of both gonopods, anterior view.

5, 1965, M-6519; under cedar bark and dew-covered moss along Hell Roaring Creek, dense forest of red cedars, fir and a few maples and spruce, July 3, 1965, M-6572; bottom of canyon near Mission Falls, red cedar, dogwood, alder, 4 mi E of St. Ignatius, July 9, 1966, M-6542; in contrast to these forested sites a collection was made by Ken Teberg from between rocks just above the splash zone of cascading water exposed to the sun, 5000 ft, 8.5 mi SE of Swan Lake guard station. Aug. 2, 1965, M-6536; copulation was observed on moss after a night of sprinkling rain, meadow rue, violets, cow parsnips, fairy bells, wild rose, spruce, and lodgepole pine in a burn area, a salamander *Ambystoma macrodactylum* collected nearby, 3500 ft, Goat Creek, R17W, T23N, 10 mi S of Swan Lake, June 26, 1965, M-6579 and M-6565; moist moss, some of four different species copulating by Big Knife Creek near a natural salt lick, 5 mi from Arlee, Apr. 25, 1965, M-6563; under and in rotton wood in a ponderosa forest by Dog Creek, June 26, 1965, M-6524; under bark at base of talus slide; also a salamander *Thamnophus elegans* in area, red cedar, lodgepole pine, ponderosa pine, 3700 ft, Jocko Creek, Cedar campground, June 28, 1965, M-6571; by low dry Schmidt Creek, Douglas-fir, larch, *Abies,* vine maple, 4000 ft, 3.5 mi from Swan Lake road, June 26, 1965, M-6573; Daphnia Pond by Big Fork, July 20, 1960, M-6575, R. H. Russell; Methodist camp W side of Flathead Lake, Rollins, May 1, 1965, John Weida; McDonald Peak, Aug. 1952, D-152; Mission Reservoir, St. Ignatius, Apr. 6, 1947; Mission Cirque, May 2, 1948, D-848, the three preceding all collected at 3700 ft, T18N, R19W; 3200 ft, McDonald Cirque, T19N, R19W, near St. Ignatius, Apr. 6, 1947, D-347, and June 23, 1950, D-350; Lake Mary Ronan, T25N, R22W, S22, May 23, 1948, D-1648, and May 23, 1948, D-1848. Missoula Co.: near Smith Creek, red cedar, aspen, spruce, *Abies,* dogwood, cottonwood, *Clintonia, Ambystoma macrodactylum* nearby in rotten material, 4200 ft, near Condon ranger station, June 27, 1965, M-6574; under mossy rocks by stream near roadside, cottonwood, spruce, Douglas-fir, larch, *Clintonia,* 1 mi below Smith Creek, June 27, 1965, M-6576; low mossy area under rocks and logs, area probably a stream during rainy periods, Crazy Horse Creek, start of trail to Turquoise Lake, 5000 ft, Mission Wild Area, July 18, 1965, N-6535; under logs, Pattee Canyon Recreation Area, May 22, 1965, M-6566; 4 mi up rock creek, June 20, 1965, M-6510; Mt. Sentinel, Missoula, May 6, M-6582, R. H. Russell; Miller Creek, Missoula, May 11, 1947, D-747; Nine Mile Creek, Huson, Apr. 21, 1948, D-748. Sanders Co.: forest of red cedar, Douglas-fir, larch, 1 mi W of Noxon near graveyard, June 17, 1966, M-6568, and May 2, 1965, M-657; by Finnigan Creek, red cedar, devils club, 2 mi W of Noxon, June 17, 1966. Idaho: Idaho Co.: in a weep area on an otherwise dry hillside facing S, ponderosa pine, Douglas-fir, vine maple, in weep area, 2800 ft, Clearwater River watershed, 3.1 mi W of Surveyor Creek, July 26, 1965, M-6570.

The specific name honors M. J. Elrod, an early Montana naturalist credited with finding the species. Specimens in the present collection were found by him at Yellow Bay, Lake Co., June 24, 1915, M-6580, and Big Fork, Flathead Co., June 30, 1919, M-6583. The species has also been recorded from Stevens Co., Washington.

Orophe cabinetus Chamberlin

Orophe cabinetus Chamberlin, 1951, Chicago Acad. Sci. Nat., Hist. Misc., No. 87:3, figs. 8,9.
Chipus unicus Loomis, 1953, Journ. Washington Acad. Sci., 43:421, fig. 18.
Orophe unicus Hoffman, 1964, Trans. of the Amer. Entomol. Soc. 90: 301-311.

Remarks: There are four main regions where *Orophe* has been collected, and each of them is roughly equidistant from at least one of the other areas. From three of the four areas both *Orophe unicus* and *Orophe cabinetus* have been collected. They both, however, probably are members of the same species, *Orophe cabinetus,* which was described first. While examining a slide of the gonopods of *Orophe unicus,* the preparation dried and the terminal elements of the gonopods changed shape, and to all intents and purposes, the *O. unicus* had changed into *O. cabinetus.* The similarities between the *Orophe* seem much closer than any differences mentioned by Hoffman (1964). Therefore they will both be considered as members of the same species.

Ecology: Two of the four regions of collection have forests with red cedar. Perhaps all four areas contain red cedar. The Noxon region had thick humus. All collections were made at elevations ranging from 2000 to 4000 ft. Probably future collections will connect these populations and result in *Orophe cabinetus* occurring along the West slopes of the Bitterroot Mountains, and Eastward up the watershed of the Clark Fork River. The Flathead Lake population is probably more isolated than the other populations due to a lower rainfall and intervening forests which are in general more xeric.

Range and Ecology: The type locality was Clarks Peak, Sanders Co. Clark mountain is S of Thompson Falls and may be what was referred to as Clarks Peak by the collector B. Malkin who also collected this species on Koo-Koo-Sint Ridge which is E of Thompson Falls. Also collected on West Fork of Emerald Creek, St. Joe National Forest, Shoshone Co., Idaho by A. Gibson. Our collection has extended the range to include Lake Co.: Lake Mary Ronan, May 23, 1948, D-1648; Methodist camp near Rollins, 2950 ft, May 1, 1965, M-6546, John Weida; Sanders Co.: Finnigan Creek, 2 mi W of Noxon, red cedar and devils club, under moss and humus, June 17, 1966, M-6567, and Aug. 9, 1965, M-6569; 4 mi W of Thompson Falls along Prospect Creek, May 1, 1949, D-849; 1 mi W of Noxon by graveyard, red cedar, Douglas-fir, larch, sunny morning, millipeds were crawling on damp earth, June 17, 1966. Collected at same location May 2, 1965, M-657.

Nearctodesmidae

Of the two species and one variety of nearctodesmids in Montana, *Ectopodesmus cristatus* seems to occupy a more mesic mountain forest than *Kepolydesmus anderisus* Chamberlin which usually occurs in very moist areas within the drier mountain forests. *E. cristatus* occurred jointly with *K. anderisus* in 4 out of the 22 sites where *K. anderisus* was collected.

Ectopodesmus cristatus, new species

Holotype and 6 other males, 11 females, junction of Clark Fork River and Deep Creek, Missoula Co., Oct. 24, 1964, M-6525.

Diagnosis: Very closely related to the geographically distant *E. remingtoni* Hoffman, but minor divergences of the gonopods and lack of dentations on keels of segments 2-4 appear to justify specific recognition. A submarginal ridge or crest on the keels, not mentioned for *remingtoni,* is probably the outstanding character.

Description: Sexes differing little in size or shape but males with surface of keels more inflated, anterior and posterior surface of the metazonites more convex, emphasizing the median transverse depression. Length of largest specimen, a female, 22 mm, width 2-3 mm; living color probably pinkish-brown.

Head with surface densely setose to above antennae; vertex minutely short-setose, median sulcus very faint. Antennae separated by less than twice the diameter of a socket. Segment 1 with a series of about 16 medium-sized setae along anterior margin, a few similar ones scattered over surface; margin with a fine rim except for a short distance at middle, in front, and a longer distance behind.

Succeeding segments with anterior corners broadly rounded; posterior corners of segments 2-7 or 8 rounded in male, not produced caudally until about segment 15; fewer anterior keels of females with back corners rounded, caudally produced from about segment 10. Keels well developed, not ridge-like on caudal segments but small on segment 19 which has each posterior corner tiny and only a little produced; keels with outer margin smooth, lacking dentations, a marginal rim continuous to near posterior angle but not around it, surface just mesad of its posterior third raised into an elongate crest from the outer posterior face of which the pore opens, Figure 3; posterior margin rimmed to near outer corner. Metazonites crossed by two series of setae which decrease in size caudad from those of segment 1, all more or less evanescent, especially on posterior half of body; about 8-10 setae in each series; first series considerably in front of transverse depression, second series about same distance behind it. On segment 19 the caudal row of 8-10 setae is marginal and prominent, directed obliquely caudad.

Gonopods shown in Figures 4-6 differ only in minor details from those of *remingtoni.*

Females with anterior ventral margin of segment 3 abruptly elevated behind coxae of second legs, the apical half usually suddenly bent forward into a rounded lip partially covering the coxae.

Ectopodesmus cristatus dentatus, new variety

Holotype, 5 other males, 4 females, rock slide W of river, 3 mi N of Thompson Falls, Sanders Co., T22N, R30W, S36, May 1, 1965, M-655; 2 males under stump, N side of Middle Thompson Lake, T26N, R27W, S4, Lincoln Co., May 2, 1965, M-659.

Diagnosis: This variety is distinguished from *cristatus* in having both corners of the keels of segments 2-5 more angular and the lateral margin straighter and with 2-3 dentations.

Ecology: This milliped occurs most commonly in the ravines or on the slopes of mountains. The wide range includes the watersheds of the Kootenai, Clark Fork, and Missouri rivers, and includes eight Montana counties and one Idaho county. The range is from elevations of 2000+ ft in the NW to 5700 ft farther SE. The most common refuge was under rocks (8 records), and others were collected under logs (2), debris (2), under boards (1), under a stump (1), in rotten wood (1), and under moist moss (1). At night in moonlight, two collections were made on moist moss near fast mountain creeks. At least 13 records were by creeks, near lakes (4), by a roadside (2), and in a field (1). Five were in forests which include spruce, three in forests made up in part of red cedar, and one included sagebrush, aspen, and lodgepole pine.

Interestingly enough, the only previous area where *Ectopodesmus* has been collected has been a cave in western Illinois. Hoffman (1962) considered *Ectopodesmus remingtoni* to be a relict survivor from a "wider Nearctodesmid distribution in the middle Tertiary." He felt that the earlier range was destroyed by a more arid climate and later by glaciation. Hoffman also pointed out that except for the Illinois *Ectopodesmus,* all other Nearctodesmidae occur in the northwestern United States.

Distribution and Habitat Records: Granite Co.: under a rock in opening of mine shaft, Douglas-fir, Engelmann spruce, lodgepole pine, Colima, near Garnet, July 22, 1965, M-6593; under boards and rocks within 250 ft of dwellings, in gully near small creek, sage, aspen, lodgepole pine, 5600 ft, American Sapphire Gem Mine off of Highway 38, T6N, R16W, S27, Aug. 6, 1965, M-65114; elev. 3800 ft, Kitchen Creek off of Rock Creek, T11N, R16W, S18, April 26, 1949, D-649. Lake Co.: elev. 3700 ft, Mission Cirque, near Saint Ignatius, T18N, R19W, S12, May 2, 1948, D-948; Mission Reservoir near Saint Ignatius, T18N, R19W, S11, Mission Mountains, June 28, 1949, D-1249; Lake Mary Ronan, T25N, R22W, S22, May 23,

1949, D-1848. Lewis and Clark Co.: in rotten wood, N facing slope covered with moss, spruce, and fir, elev. 4700 ft (this elevation was 1673 ft below Stemple Pass and is E of the Continental Divide in the watershed of the Missouri River), close to Gould Creek, on Stemple Pass Road just past junction of 279, July 13, 1965, M-6534. Lincoln Co.: under a stump, N side of Middle Thompson Lake, T26N, R27W, S4, May 2, 1965, M-659; at foot of talus slope on a talus plateau, slight flow of water, gooseberries, Kootenai River drainage, 8.5 mi W of Libby on Highway 2, Aug. 10, 1965, M-6595; under rock on mossy talus slope above a mine, Leonia, border of Idaho and Montana, Aug. 10, 1965, M-6589. Mineral Co.: Petty Creek, Alberton, T14N, R23W, S26, May 15, 1948, D-1448. Missoula Co.: by creek, red cedar, aspen, Englemann spruce, grand fir, cottonwood, dogwood, two *Ambystoma macrodactylum* were in rotten wood nearby, 4200 ft, Smith Creek in area of Swan Lake by Condon ranger station, June 27, 1965, M-6574; under rocks and logs, junction Clark Fork River with Deep Creek, T14N, R21W, S35, Oct. 24, 1964, M-6525; 3300 ft, Marshall Creek, E Missoula, Apr. 18, 1948, D-448, 3500 ft, roadside McNamara T13N, R16W, S6, Apr. 24, 1950, D-250; Kitchen Creek by Rock Creek Apr. 26, 1965, M-6587, and same location, Apr. 17, 1965, M-65130, R. H. Russell; in a field, Miller Creek 10 miles from highway, R19W, T39N, Apr. 10, 1965, M-6590, R. H. Russell; in debris, .5 mi S of Clay Bridge, Bitterroot River, Apr. 10, 1965, M-6597, R. H. Russell; W face of Mt. Sentinel, Missoula, May 5, 1965, M-6581, John Turner; O'Brien Creek, T13, R20; July 18, 1965, M-6592, Mt. Parsons. Ravalli Co.: at night on moist moss, large snails nearby, spruce, thimbleberry, Black Bear Camp, Daly Creek, by state Highway 38, T5N, R19W, S24, Aug. 6, 1965, M-6594; at night on wet moss near stream, fast cataract, moon, spruce, fir, gooseberry bushes, 5700 ft, 2 mi W of Skalkaho Falls, Aug. 6, 1965, M-6549; under rocks, flat area by creek, area mossy but not over the rocks, creek precipitous, spruce, gooseberry, lupine, pearly everlasting, about 3 mi E of Skalkaho Falls by Highway 38, T26N, R18W, S24, probably Dam Creek, Aug. 6, 1965, M-65124. Sanders Co.: rock slide W side of river, 3 mi N of Thompson Falls, T22N, R30W, S36, May 1, 1965, M-655; 4 mi W of Thompson Falls along Prospect Creek, T21N, R30W, S23, May 1, 1949, D-949; under rocks and debris, red cedar, Douglas-fir, larch, 1 mi W of Noxon near graveyard, T26N, R33W, S17, May 2, 1965, M-657; by splash zone or else under moss by rocks under wet moss near stream, red cedar, devil's club, thimbleberry, Finnigan Creek, 2 mi W of Noxon, June 17, 1966, M-6567; *Mnium* moss, larch, wet wood litter same creek by Bill Finnigan's home, Aug. 9, 1965, M-6569. Idaho: Bonner Co.: under rock, on shore left by receding water, Pend Orielle Lake, resort area, East Hope, June 17, 1966, M-6577.

Kepolydesmus anderisus Chamberlin 1910

Ecology: Collected west of the Continental Divide in the watersheds of the Clark Fork and Snake and east of the divide in the watershed of the Missouri. Previously collected by Chamberlin in three Idaho counties: Latah, Kootenae, and Idaho. In Montana the range includes Sanders, Mineral, Lake, Ravalli and Lewis and Clark counties. The elevation is from approximately 2400 to 5050 ft. The most common refuge was under rocks with eight records, and five of these sites beneath rocks were very moist, others were collected on moss (3), under wet moss (2), in, under, or by rotten wood (3), on wet rocks (1), and under wet leaves (1). Many were by creeks or weeps (10), some were by lakes (2), rock slides (2), or on the canyon floor. Nearby forests ranged from the mesic red cedar, devils club association to the more xeric ponderosa pine or lodgepole forest. Copulation was observed on Apr. 25, 1965, and on July 26, 1965. This species was also observed three ft. above the ground on the trunk of an alder.

Distribution and Habitat Records: Sanders Co.: Nine males, 6 females, from rock slide on W side of river, 3 mi N of Thompson Falls, T22N, R30W, S36, May 1, 1965, M-655; by splash zone and near stream by wet rocks under moss (either this species or *E. cristatus* or both), red cedar, devils club, Finnigan Creek 2 mi W of Noxon, Aug. 9, 1965, M-6569; under rocks near lake shore, S shore Rainbow Lake, T20N, R25W, S3, May 1, 1965, M-654; Prospect Creek, T21N, R30W, S23, 4 mi W of Thompson Falls, May 1, 1949, D-849. Lake Co.: beneath rocks on humus or rich moist soil and also at edge of rotted stumps and many near stream on green moist moss, many of them paired and copulating. This area is near a natural salt lick visited by deer, Big Knife Creek, 5 mi from Arlee, Apr. 25, 1965, M-6563; Lewis and Clark Co.: in rotten wood and in moss, 4700 ft, this area is in the Missouri watershed and is E of the Continental Divide, just past junction 279 on Stemple Pass road, July 13, 1965, M-6534. Mineral Co.: very young, Sesame Creek, NE of Saint Regis, July 3, 1965, M-6533; 1 mi N of Crystal Lake, 6 mi S of DeBorgia, July 31, 1965, M-6584, R. H. Russell; Deer Creek, 2 mi S of DeBorgia, July 31, 1965, M-6591; Petty Creek, T14N, R23W, S26, Alberton, May 15, 1948, D-1448. Missoula Co.: Six Mile Creek, T15N, R22S, S23, Huson, Apr. 21, 1948, D-648; Greenough Park, Missoula, May 8, 1950, D-1050; Blackfoot Pond, T13N, R17W, S3, Bonner, 3380 ft, May 11, 1948, D-1348. Ravalli Co.: under rotten log on canyon floor, area rich in moss with lodgepole pine, spruce, alder, and one red cedar, 5050 ft, Lost Horse Creek, July 24, 1965, M-6531; at base of dry talus slide without vegetation other than a little moss, in small moist areas where some moisture remained along with a little moss, dirt, and humus, in an adjacent area *Spirea lucida* formed the common ground cover, 4400 ft, Lost Horse Creek, July 25, 1965, M-6585; Warm Springs campground, June 21, 1965, M-6588. Idaho: Idaho

Co.: common under rocks where damp, most were very close to water and in a very moist area on a dry day, some were on wet moss where water was seeping, three pairs were copulating, one individual was three feet up on a mossless alder which was 3″ in diameter, Douglas-fir *Abies* sp., current, ocean spray, very dry in the area away and yet close to the canyon. The canyon was 10-15 ft across in places, 3050 ft, Surveyor Creek, a tributary of Clearwater River, July 26, 1965, M-6527; under rocks by weep creek entering Clearwater River at 2800 ft elevation, hillside dry with ponderosa pine, small Douglas-fir, vine maple in weep area, 3 mi W of Surveyor Creek, July 26, 1965, M-6570; under rocks almost in splash zone by cataracts, *Abies* sp., Douglas-fir, alder, dogwood, vine maple, not far from garbage dump also on Falls Creek, town of Falls Creek, July 26, 1965; under rocks on moist floor of dry precipitous creek, or moist seep having a few pools, millipeds fast, lodgepole pine, Douglas-fir, *Abies* sp., 1 mi W of Elk City turn off near Elk City; on moss and under rocks, abandoned short mine shaft, S facing slope, Lochsa burn country, 17 mi E of Lowell, July 26, 1965, M-6530.

Polydesmidae

Polydesmus inconstans Latzel 1884[3]

Distribution and Habitat Records: Missoula Co.: Four males, females, 2 young under debris at edge of Clark Fork River, Montana State University campus, Missoula, Apr. 15, 1965, M-6526; Missoula T13N, R19W, S27, Apr. 31, 1962, M-65129, Ron Garten. Flathead Co.: 1 mi E of Creston, July 4, 1965, M-65128, R. H. Russell. Lake Co.: Mission Cirque, T18N, R19W, S12, near Saint Ignatius, May 2, 1948, D-948. Idaho: Bonner Co.: Under a log, Pend Orielle lakeshore, East Hope, June 16, 1966, M-6596.

Ecology: Chamberlin and Hoffman (1958) state that this species occurs across North America in cultivated areas. It was introduced from Europe. Judd (1967) found this species near London, Ontario, in 12 of 26 localities which were each visited three times during 1964. The localities included areas such as: a greenhouse, a dump on a river, ponds, and swamps. Apparently all of the localities had water in the vicinity, but without seeing the complete records this is impossible to state with certainty. Within these localities it was found under rubbish and boards, sticks, leaves and logs, under a basket, and under a puffball. It may be that *P. inconstans* requires water nearby. In our collection it occurred close to the bank of the Clark Fork River in Missoula, under debris, old clothing, and boards. In Idaho it was found under a log on the shores of Pend Orielle Lake.

Scytonotus amandus Chamberlin 1910[4]

Distribution and Habitat Records: Lincoln Co.: Male and 5 females, Bull Lake campground, T29, R33W, S23, May 2, 1965, M-6513; foot of talus slope on a talus plateau, slight flow of water, gooseberries, N aspect, 8.5 mi W of Libby, Highway 2, Aug. 10, 1965, M-6595; under moist moss in humus by stream, many snails also, red cedar, larch, white pine, spruce, Zulu Creek, South Fork Yaak River, Aug. 10, 1965, M-6555. Mineral Co.: Under rocks by creek, lodgepole pine forest, 3600 ft, Packer Creek, Saltese, Aug. 24, 1966, M-6545.

Ecology: Previously collected in canyons of the Wasatch Mountains in Utah and Idaho, it also occurs in the mountains in Montana. Many other species of *Scytonotus* also occupy mountain habitats in other states. In Montana *S. amandus* was collected from the watersheds of the Kootenai and the Clark Fork Rivers in moist microenvironments. These areas are in the extreme west within forty miles of Idaho.

Julida

The two Montana members of this order, *Aigon parvior* (Chamberlin) and *Bollmaniulus montanae* (Chamberlin), appear to require less moisture than the other Montana millipeds.

Paeromopidae

Aigon parvior (Chamberlin)[5]

Five males, 7 females, 4 mi up Rock Creek, Missoula Co., June 20, 1965, M-6510.

In the M-6510 group only one or two specimens attaining 3 mm in diameter; number of segments 64-73. Segment 1 sparsely setose; posterior half of metazonites with tiny short setae rising from distinct punctations, usually in a rather regular row across middorsum but more scattered adjacent to pores; a series of quite closely placed punctations, each containing a large obliquely raised seta, near posterior margin. Last segment with 4-6 large setae in front of back margin; surface elesewhere with a few minute scattered setae. Anal valves each with 2 large setae. Preanal scale with 2-6 large setae just in front of the broadly rounded apex.

While Chamberlin has mentioned setae on segment 1 in his *Paeromopus eldoradus,* on the last segment of *Klansolus socius,* and the last segment and preanal scale of the present species,

[3] *Ibid.*
[4] *Ibid.*
[5] *Ibid.*

these appear to be the only references to segmental setae in the family. However, it is suspected that segmental punctations ascribed to other species originally contained more or less permanent setae.

Ecology: Occurs most frequently by rock slides. Five out of eight specimen groups with ecological data came from rock slides, one group was under boards and steel roofing and one group was crossing a road. Collections were at elevations usually between 3000 and 4000 ft, with two exceptions, one of which extended the elevation to 4750 ft. The range includes the central part of western Montana, with one collection only from the southern part of this region.

Other Range and Habitat Records: Lake Co.: 4750 ft, Mission Hill near U. B. S., T26N, R19W, May 17, 1947, D-647, L. R. Mewaldt; crossing road in early evening at W end of lake, McDonald Cirque, Mission Mountains, July 16, 1965, M-6543; moss-covered rock slide on S facing slope halfway down lake, spruce, poison oak, July 16, 1965, M-65101; McDonald Cirque, Apr. 6, 1947, D-347; 3700 ft, Mission Cirque, near St. Ignatius, May 2, 1948, D-848; Lake Mary Ronan, May 23, 1948, D-1648; in canyon below and by side of Mission Falls, mostly red cedars, some dogwood, and alder, 4000 ft, 4 mi E of St. Ignatius, July 9, 1966, M-6542; rock slide, McDonald Cirque, Apr. 14, 1965, M-65105, R. H. Russell. Missoula Co.: under boards and a big piece of steel roofing, ponderosa pine and grass nearby, day after rain, Lubrecht Forest below ecounit 1, Aug. 4, 1965, M-6541; in rock slide, Miller Creek 8 mi from highway, Apr. 10, 1965, M-6512, R. H. Russell; rock slide, Kitchen Creek off of Rock Creek, Apr. 17, 1966, M-65102, R. H. Russell; Mt. Sentinel W side of Missoula, Oct. 17, 1964, M-6552, R. H. Russell; rock slide, Mt. Jumbo, Missoula, Apr. 19, 1965, M-65106, R. H. Russell; Kitchen Creek off of Rock Creek, Apr. 21, 1965, M-65100, and same area, Apr. 26, 1965, M-6587, R. H. Russell; O'Brien Creek, 8 mi W of Missoula, no date, M-65104; 3380 ft, Blackfoot Pond, Bonner, May 11, 1948, D-1248; Bonner, .5 mi NE of Blackfoot Tavern, Apr. 8, 1950, D-550, H. A. Demaree; W side of river, Bonner, Apr. 29, 1950, D-750, Demaree. Ravalli Co.: roadside, 4500 ft, Sula, 10 mi N of Idaho border on U.S. 93, Apr. 20, 1947, D-547. Granite Co.: Rattler Gulch by Drummond, June 6, 1950, D-1150. Previously this species was reported only from the type locality of Flathead Lake, Lake Co.

Paraiulidae

Oriulus medianus Chamberlin 1940

Range: collected 18 mi S of Dillon by Russell. This location is in Beaverhead Co. which is E of the Continental Divide and is part of the Missouri River drainage system, Apr. 24, 1964, M-65110. Previously *medianus* was collected in Montana (county unknown), and in Idaho, Wyoming, Utah, Colorado, New Mexico, Iowa, Nebraska, and S. Dakota.

Ecology: Unknown.

Bollmaniulus montanae (Chamberlin)

Bollmaniulus Verhoeff, 1926. Zool. Anz., vol. 68, p. 65.

Caliulus montanae Chamberlin, 1940. Bull. Univ. Utah, biol. ser., vol. 5, No. 7, p. 16.

Ecology: Collected from 42 localities, this species has a wide distribution and is quite common. It occurs in the watersheds of the Kootenae, Missouri, Flathead, Clark Fork, and Snake rivers. Collections were made in Lincoln, Sanders, Lake, Mineral, Missoula, Ravalli, Granite, Powell, Flathead, and Broadwater counties in Montana, and Bonner and Idaho counties in Idaho.

Most of the specimens with habitat information were collected under material of plant origin. Six groups, or 24%, were collected under logs, 3 were under bark of rotting logs, 2 under boards, 2 under magazines or rags, and a single group was under each of the following: needles, sleeping bag on ground cloth, moist leaves. One was on moss. The rest, eight or 32%, were under rocks. This species is more tolerant of dryness than most of the other Montana millipeds. Many of the specimens were collected in relatively dry habitats. Eleven sites were in either ponderosa pine or lodgepole pine or forests of both species, while only four sites were in Douglas-fir or red cedar forests. Other macrohabitats were open areas, along roads, or by rock slides. The wide distribution also indicates much adaptability to wide variations of moisture and vegetation. It is apparent that this species can be successful in drier habitats than are occupied commonly by most of the other species in Montana. The adaptability of this species is also shown by its occurrence under boards, rubbish, and rocks in areas inhabited by man.

Range and Habitat Records: Broadwater Co.: under bark of rotten log, Douglas-fir forest, Carl Creek trail near Deep Creek crossing of Highway 12, Big Belt Mountains, Aug. 23, 1966, M-6538. Flathead Co.: 5.2 mi W of Apgar turnoff, Glacier National Park, W exposure by red cedars, Douglas-fir, and birch, Aug. 11, 1965, M-65125. Granite Co.: under rocks and old rags on main street of Colima, an abandoned mining town near Garnet, Douglas-fir, spruce, lodgepole pine, July 22, 1965, M-6593; under rocks by Bearmouth Hot Springs, Apr. 24, 1965, M-65115; Bearmouth Hot Springs, Feb. 14, 1965, M-65107, Randy Miller; Bobcat Creek close to where it enters Rock Creek, June 20, 1965, M-6511. Lake Co.: base of talus slide, Douglas-fir, red cedar, lodgepole pine, 3700 ft, June 28, 1965, M-6571; thick humus area by Big Knife Creek, 5 mi from Arlee, near county line, Apr. 25, 1965, M-6563; on moss night after sprinkling rain, spruce, lodgepole pine, meadow rue, cow parsnip, wild rose, 3500 ft, Goat Creek, 10 mi S of Swan Lake, June 26, 1965, M-6565; 3700 ft, Mission Cirque, near Saint Ignatius, May 2, 1948,

D-1148; 4750 ft, Missions Hill, U.B.S., T26N, R19W, May 17, 1947, D-647, L. R. Mewaldt; Smith Canyon above Kerr Dam, Polson, July 4, 1965, M-65112, Russell. Lincoln Co.: under rock of mossy talus slope, moved quickly, 500 ft S of mine, Leonia on border of Idaho and Montana, Aug. 10, 1965, M-6589; Wolf Creek near Libby, 2550 ft, T29N, R29W, S35, June 11, 1949, D-1049. Mineral Co.: under a piece of wood, lodgepole pine forest, 3600 ft, Packer Creek, Saltese, Aug. 24, 1966, M-6545. Missoula Co.: under logs, Pattee Canyon Recreation Area, May 22, 1965, M-6566; by Smith Creek red cedar, aspen, spruce, *Abies,* cottonwood, dogwood, two *Ambystoma macrodactylum* were nearby in rotten material, 4200 ft, June 27, 1965, M-6574; under a rotten log, in a little draw, day after rain, ponderosa pine, Douglas-fir, Lubrecht Forest site 1½, just below enclosure, July 22, 1965, M-65111; under logs, rock, and bark, Pattee Canyon, Oct. 18, 1964, M-6559; under needles, ponderosa pine only trees, a few clumps of grass, no humus, many specimens, many life stages, Lubrecht Forest ecounit 1, Aug. 4, 1965, M-6540; under boards and a big piece of steel roofing, day after rain, ponderosa pine and grass, below ecounit 1, Lubrecht Forest, Aug. 4, 1965; Mt. Sentinel, T13N, R19W, S26, Oct. 6, 1949, D-1349; 3300 ft, Marshall Creek, E Missoula, Apr. 18, 1948, D-348; and roadside of U.S. 93, 10 mi N of Idaho border, Sula, T11N, R19W, Apr. 20, 1947, D-547, and 3325 ft, Turah, T12N, R18W, S1, Apr. 8, 1948, D-148; .5 mi NE of the Blackfoot Tavern, Bonner, Apr. 8, 1950, D-550, H. A. Demaree; the following were collected by Russell: Lubrecht Forest, Apr. 24, 1965, M-65109; and in a field, Miller Creek, 10 mi from highway, Apr. 10, 1965, M-6512; and Kitchen Creek near Rock Creek, Apr. 26, 1965, M-6587. The rest of the collection was by R. Schmitt. Powell Co.: under rocks, 15 mi N of Drummond on Highway 271, Apr. 24, 1965, M-65108; under moist rock by trickle of water, area muddy and trampled by cows, grassy and open with sparse forest of Douglas-fir, 5700 ft, 2 mi W of McDonald summit by Highway 12, Aug. 5, 1965, M-6544; under old magazines by abandoned cabin, Douglas-fir, spruce, lodgepole pine, juniper, grass, 5500 ft, 8 mi S, up Little Black Foot River from Highway 12, Aug. 5, 1965, M-6539. Ravalli Co.: under boards and rocks within 250 ft of dwellings, E aspect, small creek, gully, sage brush, aspen, lodgepole pine, 5600 ft, American Sapphire Gem Mine, by state Highway 38, T6N, R16W, S27, Aug. 6, 1965, M-65114; under sleeping bag on ground cloth which was located on dry bed of ponderosa pine needles, ponderosa pine and *Spirea lucida,* 4400 ft, Lost Horse Creek, July 25, 1965, M-6585; under rotten wood in ponderosa pine, Douglas-fir forest, by lily pond by Lake Como, June 21, 1965, M-6514. Sanders Co.: under logs, red cedar, devils club, Finnigan Creek 2 mi W of Noxon, June 17, 1966, M-6567; under rocks and debris near graveyard, 1 mi W of Noxon, May 2, 1965, M-657; under logs, red cedar devils club, Finnigan Creek, 2 mi W of Noxon, Aug. 9, 1965, M-6569. Idaho: Idaho Co.: under leaves at base of rock cliff where a little moist dirt had accumulated, and about 12 ft further away from Surveyor Creek than *K. anderisus,* July 26, 1965, M-6527; many millipeds of various species under rocks by a weep, otherwise dry hillside, ponderosa pine, Douglas-fir, vine maple, 2800 ft, 3 mi W of Surveyor Creek (which enters Clearwater River), July 26, 1965, M-6570. Bonner Co.: under a log on Pend Orielle Lake shore, East Hope, June 16, 1966, M-6596. Previously collected by Chamberlin at type locality of Nimrod, Montana, and Hell Gate River near Clinton, Montana.

Spirostreptida: Cambalidae

In the United States most of the species in this family are known only from the type locality. Therefore, there is little available ecological information. In the Eastern United States, *Cambala annulata* (say), a large species, has secretive habits and is found "in the deepest levels of humus deposits or in the burrows of small animals," it is found at elevations ranging from sea level to about 4000 ft "most frequently in rather dry upland oak woods, usually deep in humus but occasionally under partly buried logs and rotting stumps in dry locations" (Hoffman, 1958). Other *Cambala* spp. are common in Texas caves (Causey, 1964). Other genera of the Cambalidae have been collected in California under stones on a desert mountain slope, and under stones by the seacoast (Loomis, 1938). In Washington Co., Oregon, *Mimolene oregona* Chamberlin was collected underneath the bark of a tree stump (Chamberlin, 1941). The diminutive size of the Montana species described below made it very difficult to discover while making our collection. Its habitat ranged from 2300 to 6100 ft. In one locality it was collected under a stump.

Mimolene sectile, new species

Holotype, second male, 2 females, under stump, N side of Middle Thompson Lake, T26N, R27W, S4, Lincoln Co., May 2, 1965, M-659; female, Bull Lake Campground, T29, R27W, S23, Lincoln Co., May 2, 1965, M-6513.

Diagnosis: The generic and specific descriptions of *Mimolene oregona* Chamberlin 1941 unfortunately are short and lack details of many essential characters but the gonopods somewhat resemble those of the above specimens which are included in the genus awaiting reexamination of the holotype of *oregona* for verification of the disposition. The produced and apically split mentum appears to be a peculiar feature of these specimens.

Description: Body small, a little constricted behind segment 1: 12-13 mm long, .6-.7 mm wide; submoniliform, the metazonites strongly convex behind the interzonal constriction; holotype with 42 segments, topotype male 36, 2 females 40 and 42. In alcohol the females moderately

brown in front, with lighter maculations; considerably darker behind; males darker throughout, almost black behind, with fewer maculate anterior segments.

Head lacking vertigial sulcus but a transverse one joining eyes at their mesal angles; a row of four setae just behind sulcus, a short one being near each eye with a longer one farther dorsad. Ocelli 23-27 in a broadly oval group of poorly defined series. Antennae rather short and stout; joint 2 slender but longest, joints 3-6 of subequal length but joint 5 thickest. Gnathochilarium (Fig. 7) with mentum very broad near base but apically produced and cleft below slender promentum.

Segment 1 considerably shorter than segments 2 and 3 together; slightly emarginate at middle in front; a long lateral stria from behind the eye reaching posterior margin, several short striae below it on subventral surface, surface above with one or two abbreviated striae from posterior margin.

Succeeding segments with transverse constriction weakly evident on segment 6 or 7 but becoming broad and strongly concave thereafter, lacking pits and crossed only by the lateroventral striae of the metazonites but nowhere approaching line of pores. Surface of both segmental divisions shining, but magnification shows complete, fine reticulation; segment 1 to the penultimate with a series of small setae just in front of posterior margin.

Last segment shorter than the two preceding combined; a macroseta a short distance in front of posterior margin opposite each outer angle of preanal scale, two others equidistant above it but farther forward; apex with two macrosetae projecting back from margin. Anal valves with two setae and another pair on the preanal scale which is short, broadly and evenly rounded behind but more abruptly rounded in front; tab processes lacking.

Gonopods (Fig. 8) directed caudad outside body, mesal division of each caudally hooked at apex.

Male legs with first pair crassate, joints 2-4 very short, together about as long as joint 5, slightly exceeding joint 6 which is strongly flattened dorsoventrally, directed forward, and terminating in a large, thick, blunt claw. Second legs about half as large as those immediately following. Legs 4-7 with third joint thickened, ventrally deeply excavated from near base, the excavation continuing the length of the fourth joint also; no legs with projecting ventral processes.

Other Distribution and Habitat Records: Missoula Co.: Mt. Sentinel, W side of Missoula, Oct. 17, 1964, M-6552, Russell; Bitterroot area, Lolo, T12N, R20W, S25, Apr. 15, 1948, D-248; Six Mile Creek, T15N, R22W, S23, Huson, Apr. 21, 1948, D-548; spruce, *Abies,* some large lodgepole pine, willow, huckleberry, false hellebore, bear grass, snow near lake, 6100 ft, Elsina Lake, June 28, 1965, M-6547. Sanders Co.: red cedar, Douglas-fir, larch, one mi W of Noxon near graveyard, T26N, R33W, S17, May 2, 1965, M-657; probably under logs, red cedar, devils club, 2 mi W of Noxon at Finnigan Creek, June 17, 1966, M-6567.

Ecology of the Montana Chordeumida

Many Montana species of this order occupy habitats which are very moist. Some specimens, for example, were discovered by examining moist gravel below moss near a creek. Nearly all the Chordeumida were very fast. Once their hiding place was discovered, they quickly ran and tried to disappear from view. Some members of this order also lived at high elevations in the mountains, at times close to patches of snow. Because of their generally small size and the above-mentioned characteristics, they are difficult to collect, and often escape if the collector is not alert. In general the observed habitat and behavior agrees with conclusions drawn by Cook and Collins (1895).

Five families of the Chordeumida were collected. *Endopus parvipes* of the Trichopetalidae, and *Brunsonia complexipes* of the Conotylidae, both occur at elevations ranging to 7000 ft, in areas of mountain passes where snow may linger well into July. Another Conotylid of the high elevations is *Lophomus laxus,* which occurred at an elevation of 6850 ft in an area far South of the higher elevations where *Endopus parvipes* and *Brunsonia complexipes* were collected. *Lophomus laxus* may occupy a range with a drier macroclimate and microclimate, than the other two high elevation species.

Summaries of the habitats and distribution of the Montana Chordeumida: Conotylidae: *Brunsonia complexipes* is the most widely distributed Montana Chordeumid, and was collected in seven counties including Ravalli, Sanders, Lincoln, Flathead, Lewis

and Clark, Missoula, and Lake. The altitudinal range is from 2300 to 7000 ft in the Glacier, Mission, Garnet, Flathead, Bitterroot, and Purcell mountains. Most of these areas had *Abies* or *Picea* nearby, but among the exceptions were collections made at ecounits 2, 3, and 4 in the Lubrecht Forest which were discussed in the introduction. Seven out of 18 collections were collected at 5300+ ft. Six out of 18 were under rocks, 3 were in humus, 4 were under logs, and 3 were under moss, near creeks, or trickling water. One collection was made at Rogers Pass, a fairly dry pass on the Continental Divide in Lewis and Clark County. Most of the other areas seemed to have more moisture. *Adrityla cucullata* was collected from only one locality, a field near Missoula. *Austrotyla montana* was from 3200 to 3700 ft and 2 of the 4 records were from the West face of a lightly wooded mountain. All were collected near Missoula. *Corypus cochlearis* was collected by wet rocks near a creek close to Noxon, and was also collected at a rockslide near Bonner. *Taiyutyla curvata* was collected from only one locality, a campground by a lake, at 3600 ft in Lincoln County. *Lophomus laxus* was at 3000 to 6850 ft in four counties. Nine of the 10 records were S or E of Missoula. One of the 10 was from Lake Mary Ronan in NNE Lake County, an area in the rain shadow of the Flathead Mountains and with a resultant rainfall closer to the area S and E of Missoula. The macroclimate seems drier than the macroclimate in most areas where *Endopus parvipes* and *Brunsonia complexipes* occur. Four out of 6 with habitat information were under rocks, in humus, or beneath moss associated with a rock slide, 1 of 6 was on wet moss at night near a stream, and 1 of 6 was under a log. Macromastidae: *Macromastus marginandus* was discovered by prying rocks away from the wall of a damp mine shaft in an area made desolate years before by a forest fire. Perhaps the mine shaft may be a refuge in an otherwise hostile local environment. Striariidae: *Striaria* sp. was found by a creek near Noxon. Tingupidae: *Tingupa intergerina* was under boards and rocks in a woodless dry cattle-grazing field in Sanders County. Trichopetalidae: *Endopus parvipes* was found at high elevations 6800 to 7000 ft, under bark of logs, in the Mission Mountains. Patches of snow were nearby on July 4, 1965. At Hell Roaring Pass specimens were under logs which were sunk about an inch into the soil in an alpine fir and white pine forest. They were also collected at Ecounit 6 in the Lubrecht Forest in leaf litter by hawthorne shrubs in a very moist, flat area at 4100 ft. *Orthogamus oculatus* was found only in the Noxon area near Finnigan Creek, and in an area of vegetation similar to that of the Pacific coast.

Conotylidae

This previously quite homogeneous family is here being split into two subfamilies, the first composed of the genera listed by Hoffman, 1961, through synonymy, as *Adrityla* Causey 1961, *Austrotyla* Causey 1961, *Conotyla* Cook 1895, *Proconotyla* Verhoeff 1932, and *Taiyutyla* Chamberlin 1952 of which no mention was made but which should be included in this subfamily on the basis of Chamberlin's having associated it with *Conotyla,* and his statement and illustration of the ninth male legs. Two new monotypic genera are here added to the subfamily. Hoffman did not place *Bollmanella* Chamberlin 1941 in any family, saying its type species, *oregona,* was based on a female whereas it was a male with the short and unillustrated description definitely suggesting membership in the family but not in which subfamily. The second subfamily is based solely on a new monospecific genus hereafter described.

Conotylinae, new subfamily

This subfamily is based on the previously known characters of the family.

Adrityla cucullata, new species

Holotype male, female in a field, Miller Creek, 10 miles from highway, Missoula Co., Apr. 10, 1965, M-6590, Richard Russell coll.

Diagnosis: Closely related to *A. deseretae* (Chamberlin) but with obvious differences of the gonopods (see Causey 1961).

Description: Male 22 mm long, female 20 mm long, each 3 mm wide; male flatter above than female.

Characters of head and body essentially as in *deseretae* but differences show in the gonopods, the anterior ones being higher, more slender, apex oblique, the median mesal spur on the posterior face rather than on its inner edge, the two gonopods united by an undivided sternum (Fig. 9). Posterior gonopods (Figs. 10 and 11), as compared with Figure 3, $C7^2$ of Causey 1961, have each of the inner parts a distinct flagellum, and in posterior view the outer part is not apically enlarged of tuberculate; from its base an inwardly curving structure rises, the apical portion somewhat resembling an inflated terminal joint of a leg, being dark, highly chitinized, and with a small claw. In Causey's Figure 4 this structure is called the telopodite, "T" of leg 10 and numbered $S8^1$. The parts Causey labelled T, $S8^1$, $C8^1$ in *deseretae,* do not appear disconnected in *cucullata* from the basal portion of the ninth leg and, furthermore, body segment 8 has two parts of normal legs, the anterior of which has a nipple-like tubercle behind, on each second joint. The high and thick process that is bent back over the coxa of the succeeding leg is somewhat spongy beneath its apex, instead of being setose or laciniate as in *deseretae.*

Austrotyla Causey 1961

Sonoratyla Hoffman 1961. New synonymy

Austrotyla montani, new species

Eleven males (1 the holotype), 13 females, under rocks and logs, junction of Clark Fork River and Deep Creek, Oct. 24, 1965, M-6525; male, Marshall Creek, E Missoula, Apr. 6, 1950. H. A. Demaree, D-950; 2 young, W side Mt. Sentinel, Oct. 17, 1964, R. Russell, M-6552; female, same locality as last, May 5, 1965, John Turner, M-6581; all localities Missoula Co.

Diagnosis: Closely related to *A. montivaga* (Loomis) but with differences of the gonopods and location of lobe of fourth joint of male legs 3 and 4.

Description: Largest male (holotype) 8 mm long; largest female 11 mm long; thus slightly smaller than either *montivaga* or *A. specus* (Loomis).

Eye group subtriangular, ocelli 18-20, in four series as 2, 4, 6, 8, or 3, 4, 5, 7, beginning nearest antenna. A fairly large and definite promentum present above a broad, subbasally depressed mentum.

Anterior gonopods (peltogonopods), more like those of *specus* in front view, being somewhat separated, narrower, more nearly parallel-sided, and apex subtruncate rather than rounded; obviously differing from the other species in lateral view (Fig. 12). Posterior gonopods essentially as in other species. Male legs 3 and 4 with joint 4 swollen, the ventral digitate process large and nearer distal end of joint than in those species. Coxae of tenth legs each with a long subcylindrical process in front, slightly constricted near middle, projecting forward between second joints of gonopods and the outer edge of peltogonopods.

Brunsonia, new genus

Type species: *Brunsonia complexipes,* new species

Diagnosis: Systematic position apparently between *Conotyla* Cook and Collins, and *Austrotyla* Causey, the latter genus antedating the synonymous *Sonorotyla* Hoffman, 1961 by three weeks. The two divisions of the gonopods of *Brunsonia* more closely resemble those of *Conotyla,* while their large sterna suggest association with *Austrotyla.*

Description: Size small; color much restricted; segments 30. Grouping of ocelli quadrangular rather than triangular. Antenneal joints of increasing length as follows—1, 7, 6, 2, 4, and 5 subequal, 3.

Lateral keels not strongly projecting.

Anterior gonopods (peltogonopods) rather broad, quite simple, and separated by the broad apical truncation of the well developed sternum. Posterior gonopods with each coxal joint large and much more complex than in *Conotyla,* the outer joint as in that genus, directed cephalad; sternum large and transversely subreniform.

Male legs 4, 5, and 6 with a rounded tubercle on ventral face of fourth joint. Coxae of tenth legs distally broadened, the inner two-thirds of each perforated and supporting a fleshy sack-like structure. Large third joint of eleventh legs with a long cylindrical tubercle on inner side at base, directed mesodorsad.

Brunsonia complexipes, new species

Male holotype and 7 immature males and females under and in rotting logs, Bull River Campground, 4 mi NW of Noxon, Sanders Co., T26N, R33W, S3, May 2, 1965, M-656. Other Records: Flathead Co.: one under moss by trickle of water, other under a rock, red cedars, devils club, hemlock, 3.5 mi NE Avalanche Campground, Glacier National Park, 3500 ft, 1 male and 1 female, Aug. 11, 1965, M-6550; Lake Co.: under cedar bark and moss, on a rock along with centipedes and pseudo scorpious, red cedars, *Picea* and *Acer,* Hell Roaring Creek, Mission Mountains, 2 juvenile males, July 3, 1965, M-6572; Lewis and Clark Co.: under a mossy rock in a draw, alpine fir, lodgepole pine, trees small, mostly open and dry, 5609 ft, Rogers Pass, 1 juvenile, July 13, 1965, M-6528; Lincoln Co.: under moist moss in humus by stream, many snails nearby, red cedar, *Larix,* white pine, *Picea,* Zulu Creek, S Fork Yaak River Road, 1 male, 1 juvenile, Aug. 16, 1965, M-6555; Missoula Co.: under a rotten log day after rain, Douglas-fir, ecounit 4, Lubrecht Forest, 1 male, July 22, 1965, M-65118; in humus in a depression left by a recently uprooted tree, edge of Douglas-fir forest, some moss, ecounit 3, 1 male, 1 juvenile, Lubrecht Forest, Aug. 3, 1965, M-6560; Ravalli Co.: under moist duff and soil, ice below some of the rocks, N facing aspect of mossy talus slope running sharply to creek, dogwood, *Picea, Abies,* Acer, *Alnus,* 5650 ft, Nez Perce Fork of Bitter Root River, female, July 25, 1965, M-65117; females or young or both from the following localities: Flathead Co.: under a rock in humus, on a ledge near a patch of subalpine fir, asters, below Logan Pass and 1 mile W of Logan Pass, 6300 ft, Glacier National Park, Aug. 11, 1965, M-6558; Lake Co.: under rocks, a salamander also observed (probably *Ambystoma macrodactylum*) plus beetles and beetle larvae and many centipedes under bark, many alpine firs up to 2 ft in diameter, white pine and beargrass, snow covered over 50% of ground, 7000 ft, E side Hell Roaring Pass, July 4, 1965, M-6516; under rotten logs, Cedar Lake, no cedar trees, vegetation same as at Hell Roaring Pass, snow on ground, 6500 ft, Mission Mountains, July 4, 1965, M-6518; under rocks, fir and spruce, crossing of Piper Creek, 5300 ft, July 5, 1965, M-6554; E side of North Crow Creek, Piper Creek Trail, Mission Mountains, 6400 ft, July 5, 1965; McDonald Cirque, Mission Mountains, May 16, 1965, M-6561, Russell; under moss-covered humus on rock slide on S facing slope middle of lake, spruce, fir, poison oak, McDonald Cirque, July 16, 1965, M-65101; Missoula Co.: near shore of Elsina Lake, some snow still on the ground, *Picea,* alpine fir, lodgepole pine, willow, beargrass, huckleberry and false heliobore, 6100 ft, June 28, 1965, M-6547; in humus in heavy duff layer, in depression by a log, some rain after a dry spell, moss, many deciduous shrubs, ecounit 2, Lubrecht Forest, Aug. 3, 1965, M-6548; under rocks, Rattlesnake Canyon, Nov. 1, 1964, M-6562, under logs, rocks and bark, Pattee Canyon, Oct. 18, 1964, M-6559.

Description: Holotype about 10 mm long. Color mostly restricted to a narrow band down middorsum and an area on each segment extending from under side of keels to the innermost setae of dorsum. Keels not strongly projecting but evident from segment 2-27. Dorsal setae large.

Antennae only moderately slender. Ocelli 20 on each side in holotype, arranged in a subquadrangular group of 4 vertical series—7, 6, 4, and 2 ocelli counting forward toward antennae, with an additional ocellus between the lower ends of the two posterior series. Mentum rather large, simple, subtriangular, its median surface concave across basal portion.

Details of both pairs of gonopods shown in Figures 13 and 14. Anterior gonopod and sterna of both pairs shown in Figure 15. Outer joint of male legs 3-7 and 8 or more pairs behind gonopods with a pad of fine setae below on distal half. Legs 4, 5, and 6 with a small fungiform tubercle on ventrodistal third of joint 4. Coxae of tenth legs broadened and truncate at apex from the inner two-thirds of which a broad and thick sacklike process protrudes; remainder of leg continuing from outer third of coxal apex.

Corypus, new genus

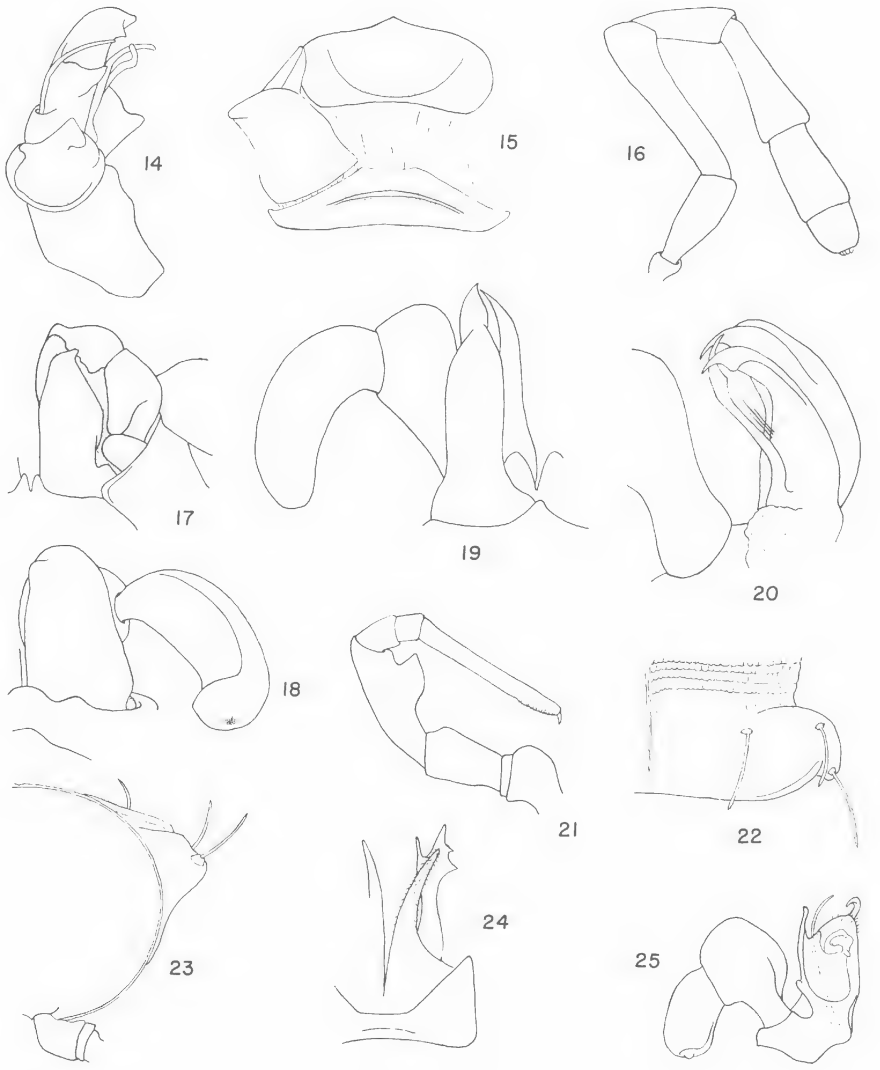
Type species: *Corypus cochlearis,* new species.

Diagnosis: Although many characters indicate association in the conotylidae, the generic position of *Corypus* is in some question as the form of all 3 joints of the ninth male legs differs from that of other genera in the family as does that of the antennae. The genus is provisionally placed in the present family.

Description: Body of medium size, composed of 30 segments, pigmented; dorsum of male flatter than in females; dorsal setae heavy, almost straight, and of moderate length; lateral keels strongly projecting, inflated above, without any margining rim. Antennae relatively short and stout. Eyes broadly triangular and containing up to 22 ocelli in four or five rows. Front of head narrow.

Anterior gonopods (peltogonopods) simple, slenderly triangular plates, shielded on the outer sides by the coxal and second joint of the posterior gonopods which form a subhemispherical or galeate structure obliquely open anteromesally. Second joint of posterior gonopods not shouldered distally; each outer joint curving up side of body in the form of a long, inwardly concave, scoop-like structure with thin lateral margins.

In outer view anterior male legs not obviously more crassate than others, but legs 3-7 with inner joints dorsoventrally thickened; seventh coxae much thickened; tenth coxae with prominent sacks.



Figures 16-18, *Corypus cochlearis.* 16, antenna; 17, left gonopods, anterior view; 18, coxal and part of second joint of left posterior gonopod with anterior gonopod at right, mesocaudal view.

Figures 19-21, *Taiyutyla curvata.* 19, left gonopods, anterior view; 20, part of second joint and coxa of posterior gonopod, anterior gonopod behind the coxa, mesocaudal view; 21, fifth male leg, anterior view.

Figures 22-25, *Lophomus laxus.* 22, right side of metazonite and part of prozonite, segment 12; 23, right half of segment 12, posterior view; 24, right anterior gonopod and sternum, posterior view; 25, right posterior gonopod, posterior view.

Corypus cochlearis, new species

Male holotype, 8 females, 2 young from cedar and devils club, Finnigan Creek, 2 mi W of Noxon, Sanders Co., Aug. 9, 1965, M-6569; 2 females, N side of river and rockslide on S side of river, Garnet Range, Bonner, Missoula Co., Apr. 29, 1950, H. A. Demaree, D-650 and D-850.

Description: Color in alcohol mostly gunmetal gray. Male 12 mm long, 1.8 mm wide; largest female 16 mm long, 2.2 mm wide; male flatter than females.

Head with clypeal-labral area narrow, sides slowly diverging upward. Antennae (Fig. 16) unusually short and stout for the family. Mentum of gnathochilarium undivided, triangular, distinctly broader than long.

On main body segments the lateral keels strongly projecting, swollen above but not rimmed. Dorsal setae long, straight, and rather heavy; outer one on each side on a swelling at posterior angle of keel; second seta on a similar swelling not far removed but dorsocephalad; inner seta considerably removed from second and preceded by an elongate swelling.

Gonopods shown in Figures 17 and 18, the anterior ones simple, narrow to an oblique outwardly directed tip. Each posterior gonopod with coxal joint high, obliquely hollowed cephalomesally; second joint strongly lobed in front; outer joint typically enlarged but curved, deeply concave throughout its length and with distinct margins, a chitinized brown spot at apex.

First 2 pairs of male legs not much smaller than next 5 pairs which do not appear crassate in lateral view but joints 3 and 4 of legs 3 and 4 are dorsoventrally thickened from front to back, especially joint 4 which has a distally directed tubercle below, near apex; coxae of seventh legs much enlarged, the distocaudal face oblique and decidedly concave with inner surface setose; joint 3 of leg 7 raised into a thick ridge along ventral side, highest head base of joint. Outer 3 joints of legs 3-7 slender, scarcely differing from those of succeeding legs, but ventral surface of outer joint of legs 3-6 somewhat spongy although not specially raised; coxae of tenth legs with large inflated sacks.

Taiyutyla curvata, new species

Male holotype, Leigh Lake Campground, elev. 3600 ft, Lincoln Co., June 14, 1949, D-1149.

Diagnosis: Apparently differing in the strongly, posteriorly curved gonopods, which also show structural peculiarities, and in several secondary sexual characters.

Description: Length approximately 10 mm. Lateral keels not strongly projecting, at most being moderate swellings of the lateral surface. Dorsal setae long and slender, the inner one each side of segments 6-27 or 28 curving dorsocaudad.

Head with about 22 ocelli in 4 rows forming a subtriangular group. Antennae long and slender, joints increasing in length as follow—1, 6 and 7 subequal, 2, 4, 5, 3. Gnathochilarium with subtriangular mentum transversely depressed near middle.

In anterior view both pairs of gonopods appear to be quite simple (Fig. 19), but in mesocaudal view they are seen to be more complicated (Fig. 20), the second joint of the ninth leg partially shown, with its coxal joint strongly produced from spongy base into two high acute branches, a heavy anterior one, the inner, posterior one much more slender. The heavy, simpler, and subequally long anterior gonopod is partially hidden by the coxal branches in the last illustration.

Male legs 1 and 2 reduced in size; legs 3-5 with basal four joints crassate, the fourth joint of leg 5 with a large conic process below (Fig. 21), a much smaller one on leg 4, but none on legs 3, 6, or 7, the two latter pairs less crassate than the three preceding ones but heavier than the postgenital pairs which are very slender, the outer joint especially so and nearly as long as joints 3 and 4 together. Coxae of tenth legs thick and with protruding sacks. Eleventh legs each with a long, slender, acute tubercle curving ventromesad from the ventrocaudal face of joint 3.

Lophominae, new subfamily

Diagnosis: Body rather loose-jointed; prozonites considerably exposed; metazonites flattened between the strongly projecting lateral keels appearing quite *Polydesmus*-like; keels with a pronounced raised rim along posterior margin. Antennae slender, the joints decreasing in length as follows—3, 5, 4, 2, 6, 7, 1. Anterior gonopods (peltogonopods) of two distinct and greatly differentiated parts. Posterior gonopods 3-jointed, the coxal joint broad, the apical portion broadly elevated and quite complicated with a long flagellum rising from its front face at base. Sternum broad, its apex narrowly separating the coxal joints. Coxae of eleventh male with a sharp process distomesally.

Lophomus, new genus

Type species: *Lophomus laxus,* new species

The characters given in the subfamily description readily allow recognition of this genus.

Lophomus laxus, new species

Eight males, 1 the holotype, 6 females, under rocks in Pattee Canyon, Oct. 18, 1964, M-6523; male, same locality, May 22, 1965, M-6566; male, 4 mi up Rock Creek, June 20, 1965, M-6510; 2 females, Blackfoot River crossing, Highway 20, July 23, 1965, M-6553; all above Missoula

Co. Male, Kitchen Creek, 3800 ft, Apr. 26, 1949, D-549; male, Kitchen Creek by Rock Creek, Apr. 26, 1965, Jay Gould, M-6557; males, Granite Co.: male, Lake Mary Ronan, Lake Co., May 23, 1948, D-1748; Flint Creek Camp, 2 mi NW of Georgetown Lake, at the base of a rock slide in humus covered with moss, spruce, gooseberry, thimbleberry, meadow rue, 5600 ft. An intensive search was made in this area of good forest cover. This is one of the closest successful collecting sites to Deer Lodge and Silver Bow Cos., M-6551, Aug. 6, 1965; male on wet moss in moonlight near a fast cataract, *Picea, Ribies,* 2 mi W Skalkaho Falls, 5700 ft, Aug. 6, 1965, M-6549; male under rocks by a precipitous creek, *Picea,* lupine, moss, pearly everlasting, and *Ribies,* 6850 ft, about 3 mi E of Skalkoho Falls on Highway 38, 1965-66, M-65124; above males Ravalli Co.

Description: Both sexes attaining length of 13 mm; body rather loose-jointed, prozonites somewhat exposed. Color light brownish in alcohol, lighter caudally; a transverse uncolored spot occupying most of inner area of keels; on back half of body a short colorless area extends along posterior margin between keels; smaller, less definite like areas elsewhere on dorsum.

Ocelli 20-25 in a triangular group of 5-7 series. Antennae long, slender, joints 3, 5, 4, 2, 6, 7, 1 in decreasing order of length, joints 6 and 7 together about equal to joint 5. Gnathochilarium with a large simple mentum.

Prozonites encircled by 4-5 sharply marked series of tiny rectangular cells or areas, rounded or scalloped behind as shown in Figure 22. Prozonites more convex than metazonites and separated from them by a broad and deep constriction. Metazonites unusually flat between keels, especially in males (Fig. 23); dorsal setae long, curved, not acuminate but almost evenly cylindrical to the abruptly pointed apex as seen in above figures. Beginning on segment 2, lateral keels become evident as swellings that increase in size thereafter to sgment 8 or 9 from which to about segment 18 they are large and prominent, projecting strongly outward from high on sides, the posterior margin with a heavy rim from base to near posterior angle (Fig. 22); keels decreasing in size behind segment 18; keels strongly convex medianly.

Beginning on segment 2 the lateral keels become evident as swellings and increase in size thereafter to segment 8 or 9 from which to about segment 18 they are large and prominent, projecting strongly outward from high on sides, the posterior margin with a heavy rim from base to near posterior angle (Fig. 22); keels decreasing in size behind segment 18; median area of keels strongly convex.

Anterior gonopods composed of two distinct elements and a large sternum (Fig. 24). Posterior gonopods with a long slender telopodite rising from near base of front face of each coxal joint which is broad, high, and ending in 2 widely separated lobes; posterior face with a contorted prominence a little below apex (Fig. 25); second joint abruptly clavate; outer joint usually typically conotyloid but in figure of holotype a tiny terminal nub is present. Male legs 4 and 5 with a small process on ventral surface of joint 4. Sterna of male segment 6 considerably wider than those of segment 5, and evenly depressed. Coxae of tenth male legs with a large rounded knob near apex of each on anterior face, mesad of this the inner corner strongly produced and perforated near apex. Eleventh male leg with inner corner of coxa produced into a long, slender, erect, acuminate projection; base of joint 3 with a large mesally directed and decurved hook surpassing the coxal projection.

Macromastidae, new family

Most closely allied to the Conotylidae but body unusually large and differing in the very prominent keels, their free margins completely and heavily rimmed; outer dorsal seta on midbody keels rudimentary. Anterior gonopods not greatly unlike those of certain conotylids but the posterior ones (ninth legs) are very widely separated by a short and wide sternum; each leg composed of 4 joints, the outer one larger than known elsewhere in the order; joints 2 and 3 about as in normal legs; coxal joint small, bearing a very long, slender flagellum in front to which the generic name alludes. Male legs 1 and 2 smaller than adjacent ones, without specializations; legs 3-7 heavier than others, lacking special processes but the outer joint evenly subcylindrical; ventral surface minutely granular or spiculate throughout and lacking setae; sterna not modified; tenth legs with coxal sacks.

Macromastus, new genus

Type species: *Macromastus marginandus,* new species

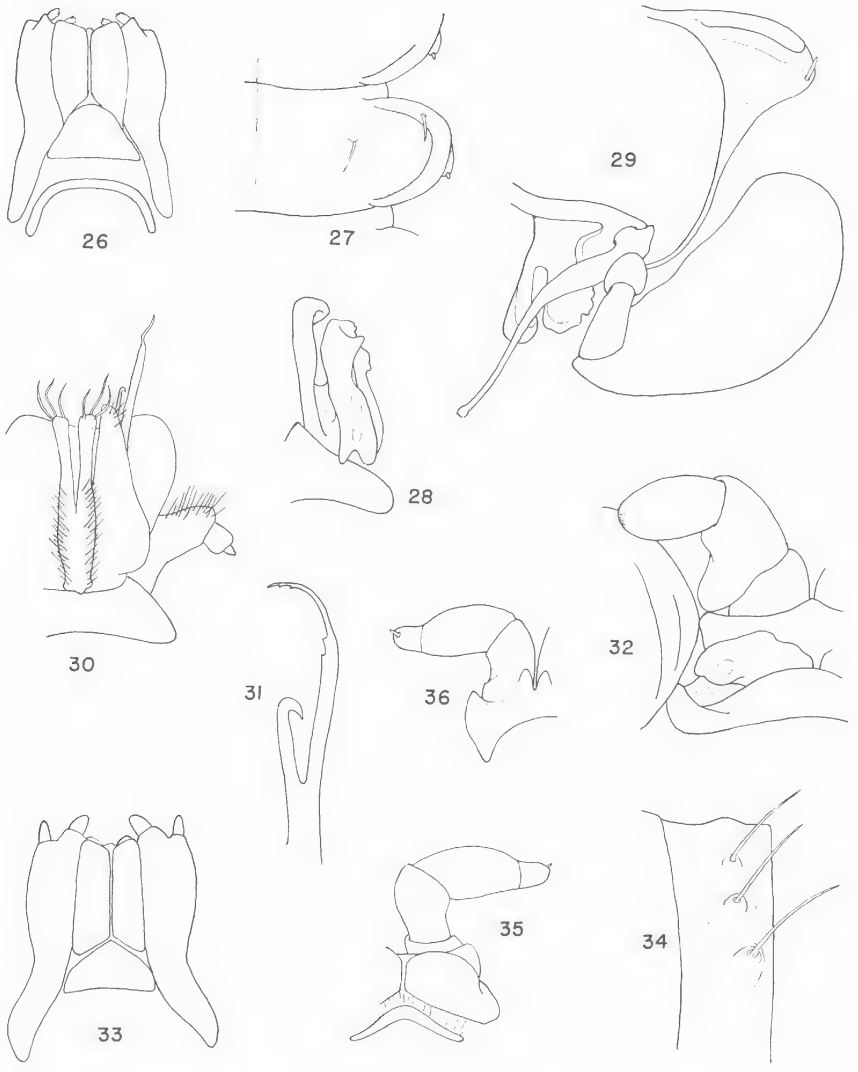
The characters given for the family are sufficient for recognition of the genus.

Macromastus marginandus, new species

Male holotype found under rock 2 ft above floor of damp, short mine shaft on S facing slope, Lochsa Burn country, 17 mi E of Lowell, on State Highway 9, Idaho Co., Idaho, July 26, 1965, M-65119, the locality less than 30 mi from nearest point in Montana.

Description: Body large and relatively broad; dorsum notably flattened; length 21 mm, width 2.5 mm.

Head with ocelli numerous, 21-22, in a triangular group. Antennae long and very slender, capable of reaching, along back, to or beyond segment 6; joints increasing in length as follows—1, 7, 6, 2, 5, 4, 3; joints 3-6 indistinctly thicker at distal ends. Gnathochilarium shown in Figure 26.



Figures 26-29, *Macromastus marginandus.* 26, gnathochilarium; 27, right half of segment 11; 28, right anterior gonopod and sternum, anterior view; 29, right gonopods and keel of segment 7, posterior view.

Figures 30-31, *Tingupa intergerina.* 30, gonopods and sternum, anterior view; 31, slender flagellum-like structure of Figure 30 enlarged, lateral view.

Figure 32, *Endopus parvipes.* Left anterior and posterior gonopods with sterna, and lower edge of segment 7 of paratype, anterior view.

Figures 33-36, *Orthogmus oculatus.* 33, gnathochilarium; 34, left side of male segment 14; 35, right anterior gonopod and sternum, and posterior gonopod with small portion of sternum showing, anterior view; 36, same posterior gonopod and sternum, posterior view.

Segment 1 a little shorter and more rounded in front than that shown in Figure 55, Cook and Collins 1895, for *Conotyla fischeri,* and with large dorsal setae in much the same arrangement except that the inner one each side is farther laterad, the space between it and the second seta only slightly exceeding the space to the median furrow; outer seta rising from slightly below lateral angle.

Body segments with keels beginning on segment 2 and continuing to segment 25, those of midbody strongly projecting, the free margins very heavily rimmed (Fig. 27), inner surface, decidedly inflated. Dorsal setae on several segments at ends of body not differentiated in size, but those at caudal end longest; from segment 6 or 7-23 the outer seta on each side is notably smaller than the inner ones, becoming rudimentary on median third of body, projecting from below rim at outer angle of keel; intermediate seta, except at ends of body, rising from forward section of marginal rim (Fig. 27); inner seta at base of keel.

Each anterior gonopod composed of 2 erect divisions, the mesal one more slender, higher, and hooded behind at apex (Fig. 28); sternum triangular. Ninth legs 4-jointed (Fig. 29), widely separated at base and rising from the outer limits of a very broad but short, curved sternum which is extended ventrad each side into a foliar lobe; the 3 inner leg joints slender, and together about half as long as the very large, swollen outer joint that extends up outer side of segment to near lateral keel; coxal joint with a long, slender, slightly sigmoidally curved flagellum extending mesoventrad from in front, its apex slightly inflated.

Male legs 1 and 2 smaller than the next 5 pairs, the outer joint finely setose below; remaining pregenital legs heavier than those following, the outer joint long, quite evenly cylindrical to the abruptly rounded tip, and minutely granulose over ventral surface, lacking ventral setae; fourth leg joints more strongly bowed than those of postgenital legs; no other specializations of pregenital legs and none on the sterna; tenth legs with inflated coxal sacks.

Striariidae

Striaria Bollman 1888

Striaria sp.

Lack of males has made identification of the species impossible, but the following records are given to show the distribution of the genus in Montana: collected close to a creek in very moist habitat under moss on wet rocks in a forest of red cedar, devils club, thimbleberry, 2300 ft, 2 mi W of Noxon at Finnigan Creek, June 17, 1966, M-6567, and on humus in same area, Aug. 9, 1965, M-6569, and M-65116. Previous range of this genus: Appalachian region, Illinois, California.

Tingupidae

Tingupa intergerina, new species

Holotype male, Marshall Creek, E of Missoula, 3300 ft, Apr. 18, 1948, D-348; female, under boards and rocks in dry grazing land 5 mi W of Dixon, Sanders Co., May 1, 1965, M-651.

Diagnosis: Most closely related to *T. pallida* Loomis but it appears to be a pigmented surface species. Gonopodial differences include having a large plate-like process, not observed in other species, in front of the ninth legs.

Description: Body dark brown in alcohol; 5.5 mm long in male, 6.5 mm in female, each with 30 segments.

Head with 10-11 ocelli in male, 13 in female, forming a subtriangular group; 1 or 2 ocelli in anterior row, 4 in middle row, and 6 or 7 behind in a row strongly bowed forward. Male antennae broken off, those of female stouter than in males of *pallida.*

Segment 1 not greatly narrower than segment 2, front margin almost evenly rounded across middle; outer limits visible from above, not abruptly descending, and with only a faintly discernible ridge above; lateral seta with base visible in outer angle from above, the 4 dorsal setae in a nearly straight transverse row, space between inner pair greater than that of either side.

Gonopods shown in Figures 30 and 31. Immediately in front of the base of the ninth legs, and rising behind the other portions of the gonopods, is a broad, high, pigmented plate-like structure, apically emarginate, thin, and concave each side in front, its median portion thickened there. No such structure has been reported in other member of the genus and, without complete dissection of the only male, it has been impossible to determine if the plate is mesally divided or where it is attached at base. Ninth legs with second joint unusually small, the terminal joint rudimentary and without apical claw.

Trichopetalidae

Endopus, new genus*

Type species: *Endopus parvipes,* new species

Diagnosis: Although associated with *Scoterpes* Cope, which Hoffman (1961) tentatively placed

* Prior to publication of this paper, Dr. Wm. A. Shear saw a carbon copy of it, which included drawings, and questioned the maturity of the holotypes on which this and the next genus were

in the above family until he could treat it in a subsequent paper, it is more closely associated with *Orthogmus,* as shown by the gonopods, but the anterior portion of metazonites not swollen; dorsal setae never in a straight, transverse row; also the lateral keels are smaller.

Description: Body of moderate size, rather stout, fusiform, little flattened, apparently not strongly pigmented, and composed of 28 segments.

Ocelli usually in 3 rows arranged in a truncated triangle. Antennae not especially long or slender. Gnathochilarium with simple mentum.

Metazonites flattened lengthwise, the dorsal setae shorter than in *Orthogmus,* and not in a straight transverse row, their basal tubercles not borne on large surface swellings; lateral keels poorly developed, little more than moderate convexities of the lateral surface. Preanal scale broadly truncate at apex.

Gonopods exceedingly simple; the anterior pair small and contained within the body; posterior ones 3-jointed, the third joint short, thick, and extending only a little over side of segment 7, lacking a terminal claw. Pregenital legs of male with no unusual modifications except that the first 2 pairs are rather small and with the usual ventral comb of setae on outer joint. Coxae of tenth male legs with a large open pore at apex.

Endopus parvipes, new species

Holotype and 4 other males, female, under bark and logs, E of Hell Roaring Pass, 6800 ft, Rainbow Lake, Lake Co., July 4, 1965, M-6517; 3 males, 6 females, under logs sunk 1″ into soil, 60 ft tall alpine fir and white pine some 2′ in diameter, snow over 50% of ground, 7000 ft, Hell Roaring Pass, Mission Mountains, July 4, 1965, M-6515; Lake Co.: moist area, badly broken parts of 4 specimens, one a section of male in leaf litter by hawthorne shrubs, Lubrecht Forest, ecounit 6, Missoula Co., July 22, 1965, M-65120.

Description: Body fusiform of moderate size, stout, little flattened; largest specimens, a female, 11 mm long, 1.5 mm wide; males shorter but same width; preserved specimens show poor pigmentation.

Head with eyes quite uniformly composed of 15 ocelli in a truncated triangle of 3 rows—7, 5, 3 another ocellus sometimes below lower 3. Antennae of moderate length and thickness; joints increasing in length as follows—1, 7, 6, 2 almost equal 4, 5 slightly shorter than 3. Gnathochilarium with mentum undivided, triangular, deeply concave across basal half; a large, greatly depressed area between mentum and hypostoma.

Principal body segments with lateral keels poorly developed, little more than moderate swellings of the lateral surface. Dorsal setae of moderate length, rising from hemispherical tubercles borne on inconspicuous surface swellings; outer seta each side at posterior corner of keel; second one in front, slightly dorsad, and less than half the distance to inner one which is directly dorsad and about twice as far from the median line. Preanal scale about twice as broad as long, apex broad, transverse or faintly concave.

Both pairs of gonopods small and very simple (Fig. 32); the anterior ones low, broad, somewhat thickened, and held within the body; posterior gonopods 3-jointed; coxal joint small; second joint much thicker at base than apex; outer joint with chitinized area at tip but lacking a claw.

Orthogmus, new genus

Type species: *Orthogmus oculatus,* new species

Diagnosis: A strictly epigean genus closest to *Scoterpes* Cope but having fewer segments, strongly developed eyes, body well pigmented, and the anterior gonopods much simpler.

Description: Body larger than *Scoterpes,* strongly pigmented, composed of only 28 segments, males more slender and with dorsum flatter than females, dorsal setae a little longer.

Eyes fully developed, in a subtriangular group. Antennae quite short and stout, third joint longest. Gnathochilarium with undivided mentum.

Segments with lateral keels well developed, evident to segment 26. Dorsal setae larger and about half as long as thickness of body, rising from large tubercles borne on swellings of the surface, the 3 setae each side of middle in an almost straight but slightly oblique line. Except on a few segments at ends of body, the metazonites are convex over much of their length but flattened for a space along posterior margin.

Anterior gonopods reduced to low, simple, subhemispherical structures. Ninth legs apparently 3-jointed, in outline much resembling those of *Scoterpes* but with the third, or outer joint, indistinct and with a tiny claw.

Pregenital legs and sterna unmodified except that outer joint of legs 1 and 2 has a comb of small setae along ventral surface. Leg 10 with pore opening inward from mesodistal face of coxa, other legs and sterna behind gonopods unmodified.

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founded. He suggested that both genera might belong in the Conotylidae. Reexamination has shown both holotypes to lack one moult of maturity, and while *Endopus* probably is conotylid, its membership in an established genus is in doubt. A female paratype of *Orthogmus,* sent to the Florida State Collection of Arthropods, in Gainesville, was found to have 30 segments but its family position is questionable although not its inclusion as a readily identifiable member of a valid new genus of the order Chordeumida.

Orthogmus oculatus, new species

Holotype male, female, 6 young, Finnigan Creek, 2 mi W of Noxon, Aug. 9, 1965, M-6569; male, 3 females, same locality, Sanders Co., June 17, 1966, M-6567.

Description: Males about 10 mm long; females to 13 mm long and 1.5 mm wide, heavier bodied and more convex. Color in alcohol grayish gunmetal.

Head with eyes composed of subequally large, well-formed ocelli in a triangular group of 4 rows—7, 5, 4, 2, counting from back of head, little variation in number of ocelli. Antennae rather stout, joints increasing in length as follows—1, 7, 6, 2, 4, 5, 3, with joints 2 and 3 more slender than any that follow. Gnathochilarium shown in Figure 33.

Segment 1 with row of setae each side bowed obliquely forward from the outer one in lateral angle to the submedian one far in front of posterior margin. On succeeding segments the rows of setae rapidly become straighter with scarcely any curve evident from segment 3 or 4 caudad, rows somewhat oblique. Setae rising from conspicuous hemispherical turbercles borne on strong swellings of surface, the 2 outer tubercles and swellings largest (Fig. 34). Except near ends of body, the metazonites with anterior three-quarters, or more, strongly convex, remainder flat. Preanal scale about half as long as wide and almost semicircular, the apex extending well beyond the 2 subterminal setae.

Anterior gonopods as described for the genus and as shown in Figure 35, which also shows ninth leg from in front where what appears to be a basal joint is part of the sternum. Ninth leg shown in back view in Figure 36. Anterior male legs and sterna unmodified except for a comb of fine setae beneath outer joint of legs 1 and 2. Tenth legs as described for genus.

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Literature Cited

Blake, G. M., R. W. Steele, and T. J. Nimlos. 1965. Study plan, Intensive hydrologic analysis of the north Fork of Elk Creek Watershed. Montana Forest and Conservation Experiment Station, Missoula: 22.

Causey, N. B. 1961. Adrityla, a new milliped genus (Chordeumidea: Conotylidae). Psyche, 68: 131-136.

————. 1961. Austrotyla, a new milliped genus (Chordeumidea: Conotylidae). Proc. Biol. Soc. Washington, 74: 251-266.

————. 1964. New cavernicolous millipeds of the family Cambalidae from Texas and Mexico. Int. Journ. of Speleology, 1: parts 1-2: 237-248.

Chamberlin, R. V. 1910. Diplopoda from the western states. Ann. Ent. Soc. Amer., No. 4: 233-262.

————. 1940. New genera and species of North American Paraiulidae. Bull. Univ. Utah, biol. ser., 5: No. 7: 1-39.

————. 1941.. New western millipeds. Bull. Univ. Utah, 31 (12): 3-23.

————. 1951. Eleven new western millipeds. Chicago Acad. Sci. Nat. Hist. Misc. No. 87: 1-12.

————. 1952. Two Oregon millipeds of the order Chordeumida. Chicago Acad. Sci. Nat. Hist. Misc., No. 113: 1-3.

————, and R. L. Hoffman. 1958. Checklist of the millipeds of North America. U.S. Nat. Mus. Bull. 266: 1-236.

Cloudsley-Thompson, J. L. 1958. Spiders, scorpions, centipedes and mites, the ecology and natural history of woodlice, "Myriapods" and Arachnids. Pergamon Press, London, England, 228.

————. 1962. Microclimates and the distribution of terrestrial arthropods. Ann. Rev. Ent., 7: 199-222.

————. 1963. Ann. and Mag. Nat. Hist., Ser. 12, Vol. 2: 947-962.

Cook, O. F. 1904. Myriapoda of northwestern North America, in Harriman Alaska Expedition, Vol. 8 (Insects, part 1): 47-82.

———— and G. N. Collins. 1895. The crasped osomatidae of North America. Ann. New York Acad. Sci., 9:1-100.

Donisthorpe, H. St. J. K. 1927. The guests of British ants. London.

Dowdy, W. W. 1968. An ecological study of some millipeds in two central Missouri communities: Ann. Ent. Soc. Amer. 61(5): 1059-1063.
Habeck, J. R. 1967. Mountain Hemlock communities in western Montana. Northwest Sci., 41(4): 169-177.
————. 1969. A gradient analysis of a timberline zone at Logan Pass, Glacier Park Montana. Northwest Sci., 43(2): 65-73.
Hannum, C. A. 1926. Anatomy of the milliped *Chonaphe armatus*. Puget Sound Biological Station, University of Washington, 5:109-119.
Hoffman, R. L. 1958. Appalachian Cambalidae: taxonomy and distribution. Journ. of the Wash. Acad. of Sci., 48(3): 90-94.
————. 1961. Systematic and morphological notes on North American conotyloid Diplopoda. Trans. American Ent. Soc., 87: 259-272.
————. 1962. A new genus and species of the diplopod family Nearctodesmidae from Illinois (Polydesmida). American Midland Naturalist, 68(1): 192-198.
————. 1964. A new subfamily of xystodesmid millipeds from North America and China (Polydesmida). Trans. of the Amer. Ent. Soc., 90: 301-311.
Judd, W. W. 1967. Millipeds (Diplopoda) in the vicinity of London, Ontario. Canadian Field Nat., 81 (3): 189-196.
Loomis, H. F. 1938. The cambaloid millipeds of the United States including a family new to the fauna and new genera and species. Proc. U.S. Nat. Mus., 86(3043): 27-66.
————. 1953. New millipeds of the western states and lower California. Journ. Washington Acad. Sci., 43(12): 417-422.
Nimlos, T. J., G. M. Blake, R. W. Steele, and R. D. Taber. undated. Available soil moisture as a determinant in the distribution and productivity of plants and animals in major forest communities. Study plan 30 p. and Progress Report 25 p. Montana Forest and Conservation Experiment Station, Missoula.
U.S. Dept. of Agric. 1941. Yearbook of Agriculture, Climate and Man. U.S. Govt. Printing Office, Washington, D.C.
Verhoeff, K. W. 1926-1932. Diplopoda, *in* H. G. Bronn, Klassen und Ordnungen des Tierreichs. Bd. 5, Abt. 2, buch 2, lief., 1-13: 1-2084.
Williams, S. R., and Hefner, R. A. 1928. The millipedes and centipedes of Ohio. Bull. Ohio Biol. Surv., No. 18, Vol. 4, No. 3. Ohio State Univ. Bull., Vol. 33, No. 7: 93-146.

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Association News

The 44th annual meeting, jointly conducted with the Idaho Academy of Science and the Washington Entomological Society and held on the campus of the University of Idaho, set new records for number of registrants (497) and number of papers presented (295). The Local Arrangements Committee, headed by Dr. Terry Armstrong of the University of Idaho, deserves special commendation for their detailed planning and extensive effort that enabled this large meeting to run smoothly.

The following individuals were elected as the new officers and trustees for 1971:

President: William Dittrich

Vice-President: Richard Clem

Secretary-Treasurer: Glenn Deitschman

Trustees: Levon Balzer, Donald Horner, Otis Maloy, Bernard Martin, Alfred Slinkard.

Awards of citations for "outstanding contributions in the field of science in the PNW" were made to Luther Cressman (Anthropology, University of Oregon), Stanley P. Gessel (Forestry, University of Washington), and Thomas M. C. Taylor (Provincial Museum, Victoria, B.C.). Chosen for 1971's Honorary Trustees were Charles J. Flora (President, Western Washington State College), Marshal T. Huntting (Division of Mines and Geology, State of Washington), and Edward B. Lindaman (President, Whitworth College). Those elected to Honorary Life Membership in the Association were Julian Barksdale (Geology, University of Washington), Charles D. Campbell (Geology, Washington State University), William T. Ferrell (Forestry, Oregon State University), and Maurice T. James (Entomology, Washington State University).

Of twenty-one applications received this year for research grants from the Association, the top seven were awarded grants of $175 each. The successful applicants were James B. States (Zoology, Washington State University), Richard Mack (Botany, Washington State University), Douglas McKeever (Geology, Western Washington State College), Clifford Wood (Geography, University of Idaho), Kenneth Knoll (Geology, University of Kansas), Rex Cates (Botany, University of Washington), and Glen Greene (Anthropology, Washington State University).

The site of next year's annual meeting will be Western Washington State College in Bellingham. Plan now to give a paper there on your results from this year's research.

Northwest Science

Raymond E. Wildung
Ronald C. Routson
and
Ronald L. Schmidt

Battelle Memorial Institute
Pacific Northwest Laboratories
Richland, Washington

Isolation and Size Fractionation of Microparticulate Matter Suspended in the Columbia River

Particulate matter sedimented in natural waters is known to exert a direct influence on solution concentration of radionuclides (Garder and Skulberg, 1964) and pesticides (Lotse *et al.,* 1968), and the importance of the role of suspended particulate matter in the sorption of pesticides from water has been recently demonstrated (Pfister *et al.,* 1969). However, relatively little attention has been directed toward determination of the influence of suspended particulate subdivision on ion sorption from solution particularly in the clay size range (less than 2μ) although total surface activity generally increases markedly with reduced mean particle diameter (Farrar and Coleman, 1967).

In order to evaluate the influence of suspended particle size on the behavior of radionuclides and pesticides in the Columbia River, a centrifugation technique was devised which allowed size fractionation of suspended particulate matter in the micron and submicron size ranges in quantities sufficient for further studies of isolated fractions but without harsh chemical treatment which might alter the properties of the individual components. The isolation method, designed for waters of low suspended sediment concentration, should be particularly applicable to surface waters of the Northwest.

Materials and Methods

Suspended particulate materials were isolated from samples (200 liter) of Columbia River water taken off-shore approximately five miles upstream from the U.S. Atomic Energy Commission Hanford reactors near Richland, Washington.

Particulate materials greater than 53μ in diameter were removed from subsamples of river water by siphoning the water through a 53μ stainless steel sieve. Particulates in the sieve effluent water were concentrated by continuous flow centrifugation of the water in a Sharples Laboratory Super Centrifuge (Model T-1) equipped with a No. 1-H standard clarifier rotor lined with cellulose acetate membrane and operated at maximum speed (23,000 rpm) which exerted a force of 13,200 *g*. Under these conditions, the flow rate through the centrifuge amounted to 60 ml/min, and the turbidity of the supernatant solution as measured on a Hach Model 1860 Laboratory Turbidimeter was reduced to a level approximating that of distilled water. Assuming a particle specific gravity of 1.52 or greater (Jackson, 1956), centrifugation under these conditions will sediment medium-fine clay with a limiting particle diameter of 0.07 micron.

At the completion of centrifugation, sediment was transferred from the liner to a volumetric flask using a small quantity (less than 5 ml) of a neutral sodium chloride solution (1.5*M*) to facilitate dispersion, and the resulting suspension taken to appropriate volume.

Particulate matter isolated from the raw river water and redispersed as described above was fractionated according to equivalent spherical diameter by centrifugation techniques. The quantity of material in each size fraction was determined gravimetrically after collection on a filter of appropriate limiting particle diameter.

Centrifugation parameters were designed to meet the requirements of Stoke's law for viscous flow about a falling spherical body, and centrifugation time intervals were calculated using the Svedberg and Nichol's integrated form of Stoke's law (Jackson, 1956) as follows:

$$t_{min} = \frac{63 \times 10^8 \ \eta \ \log_{10} R/s}{(N_m)^2 (D_\mu)^\Delta \ (\Delta s)}$$

in which t_{min} was the time of centrifugation (min), η, the viscosity (poises) at centrifuge temperature; R and S, the radii (cm) of rotation for the sediment and the surface of the suspension, respectively; N_m, the centrifugation speed (rpm); $D\mu$, the desired particle diameter (μ) and Δs, the difference in specific gravity of the solvated particle and the suspension liquid. For clay particles less than 2μ, s was taken as 2.50 and for particles greater than 2μ, s was assumed to equal 2.65 (Jackson, 1956).

A Lourdes Model A-2 Beta-Fuge, an automatic refrigerated centrifuge equipped with a No. 1100 Density Gradient Rotor and centrifugation tubes (250 ml) of the polypropylene type, was employed in the separation of particles suspended in the concentrated solution. Time intervals and centrifugation speeds required for particle size fractionation were calculated from the above equation.

After centrifugation of an aliquot of the concentrated suspension at the designated speed for the required time interval, the supernatant liquid, containing particles of diameter equal to or less than the calculated limiting diameter, was removed under vacuum using a narrow glass tube with an upturned tip and collected in a vacuum trap. The remaining sediment was resuspended in a dilute solution of sodium chloride. Centrifugation and resuspension was repeated ten times or until the measured turbidity of the supernatant liquid approximated that of distilled water. The supernates were composited for each size fraction and stored under refrigeration at 4° C for future analyses. The above procedure was repeated at centrifugation parameters appropriate to the removal of the desired size fractions. The sediment remaining after completion of centrifugation was taken as the fraction containing the largest particle diameter.

The dilute size fraction suspensions were concentrated for further characterization by addition of sufficient solid calcium chloride to result in a 0.1*M* solution to flocculate the suspensions followed by centrifugation until the supernatant turbidity approximated distilled water. After dilution to volume, the concentrated suspensions were stored at 4° C.

The concentration of solids in the size-fractionated suspensions was determined by filtration, under vacuum pressures up to 70 cm Hg, of a known volume of suspension through a dry (60° C) pre-weighed filter disc of appropriate pore size, and gravimetric determination of the dry (60° C) retained solids. The filters, both membrane

and microfiber matric types, were preconditioned by leaching with distilled water (200 ml) to constant weight. Calculation of the mean concentration of fractionated suspended matter in the concentrated suspensions included sediment concentration values obtained by evaporation of known volumes of the size-fractionated suspensions to dryness (60° C) in pre-weighed glass ampules. These were evacuated and flame-sealed before gravimetric measurement of the residues (Kittrick, 1970).

Results and Discussion

The centrifugation method described allowed isolation and reproducible size fractionation of particulate matter in sufficient concentrations for further studies of ion sorption and release. Variation in mean concentration of the fractionated suspended matter was less than 2 percent for both of the filter media employed. However, use of the fiber matric filter significantly reduced filtration time in the submicron size ranges due to increased flow rate. Turbidity values of the filtered effluent solution did not exceed those of distilled water, indicating the number of particles in each fraction having diameters less than the lower limiting diameter were insignificant. The size fractions may have contained particles with diameters greater than the upper limiting diameter, *e.g.,* algal cells and organo-mineral complexes, if these materials had a lower specific gravity than the clay minerals used as a basis for calculation of the centrifugation time. Filtration through filters of pore diameters equivalent to the calculated upper limiting particle diameter or measurement of the average specific gravity of particulate matter in isolated size fractions may be employed as necessary to assure precise definition of particle size.

Application of the procedures to size fractionation of small quantities (0.lg) of ZnS particles (less than 2μ to greater than 44μ in diameter) of known specific gravity (3.97) resulted in mean recovery of 99.7 percent of ZnS.

The determined particle size distribution of particulate matter suspended in the Columbia River after the spring freshet is outlined in Table 1. Mean recovery of

TABLE. 1. Particle size distribution of particulate matter isolated from Columbia River water after the spring freshet.

Equivalent spherical diameter (μ)	Particle size distribution	
	Concentration (mg/liter)	Fraction of total (%)
<0.2	2.6	7.5
0.5 to 0.2	5.3	15.3
2.0 to 0.5	13.0	37.5
53 to 2.0	12.4	35.8
Total	34.7	96.1

total solids in the several size fractions amounted to over 95 percent. The importance of investigations to determine the influence of clay-size particulate matter on ion behavior in surface waters was emphasized by the results of these investigations which indicated that of the particulate matter less than 53μ in diameter suspended in the river during the spring, 60 percent was less than 2.0μ in diameter or of clay size, and as much as 22 percent of the total suspended matter was in the less-than-0.5μ fraction. Materials in these size ranges may be expected to exhibit high surface areas and, if of terrestrial origin, high charge densities relative to particles larger in diameter.

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Literature Cited

Farrar, D. M. and J. D. Coleman. 1967. Correlation of surface area with other properties of nineteen British clay soils. J. Soil Sci. 18: 118-124.

Garder, K. and O. Skulberg. 1964. Sorption phenomena of radionuclides to clay particles in river water. Int. J. Wat. Poll. 8: 229-241.

Jackson, M. L. 1956. Soil chemical analysis. Department of Soils, University of Wisconsin, Madison, Wis. 991 p.

Kittrick, J. A. and E. W. Hope. 1970. Preventing water resorption in weight loss determinations. Soil Sci. Soc. Amer. Proc. 34: 536-537.

Lotse, E. G., D. A. Graetz, G. Chesters, G. B. Lee and L. W. Newland. 1968. Lindane adsorption by lake sediments. Environ. Sci. Technol. 2: 353-357.

Pfister, R. M., P. R. Dugan and J. I. Crea. 1969. Microparticulates: Isolation from water and identification of associated chlorinated pesticides. Sci. 166: 878-879.

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Temperatures and Classification of Soils in Latah, Benewah, and Kootenai Counties, Idaho[1]

The primary objective of this study was to accumulate soil temperature data to aid in the classification of soils in Latah, Benewah, and Kootenai counties, Idaho.

The new soil classification system (Soil Survey Staff, 1960 and 1967 supplement) uses criteria based on soil properties that can be observed or measured. Properties selected as diagnostic are those that either affect soil genesis or result from soil genesis. Soil temperature is an important one of these criteria, and one about which little is known for the soils in the three north Idaho counties.

The soil classification system uses soil temperature as an important criterion at the great group and family categories, and in the definition of a few suborder and subgroup classes. For instance, the cryic great groups are characterized in part by mean annual soil temperatures of less than 47°F and a mean summer soil temperature at a depth of 20 inches or a lithic or paralithic contact, whichever is shallower, of less than 59°F if cultivated or without an 0 horizon, or less than 47°F if with an 0 horizon. The most extensive use of soil temperatures as classification criteria is at the family category, where soil temperature classes are used as family differentiae in all orders, along with texture and mineralogy in most of the orders.

The soil classification system separates soil temperatures into four major classes in the family category. These four major classes, based on mean annual soil temperatures, are: frigid, less than 47°F; mesic, 47°F to 59°F; thermic, 50°F to 72°F; and hyperthermic, 72°F or more. Iso is used as a prefix to these soil temperature classes for soils having less than 9°F difference between mean summer (June, July, and August) and mean winter (December, January, and February) soil temperatures, such as isohyperthermic.

Methods

Forty sites were used in this study. Sites were selected to give a good representation of soils of the area, with emphasis on different soil orders, precipitation zones, elevation, and topography (Fig. 1). Soil profiles were examined with a tile spade and soil auger to ascertain their characteristics with reference to a defined soil series. Soil

[1] Idaho Agricultural Experiment Station Research Paper No. 837. Contribution from the Department of Agricultural Biochemistry and Soils, University of Idaho. Portion of an M.S. thesis of senior author, University of Idaho, Moscow, 1969.

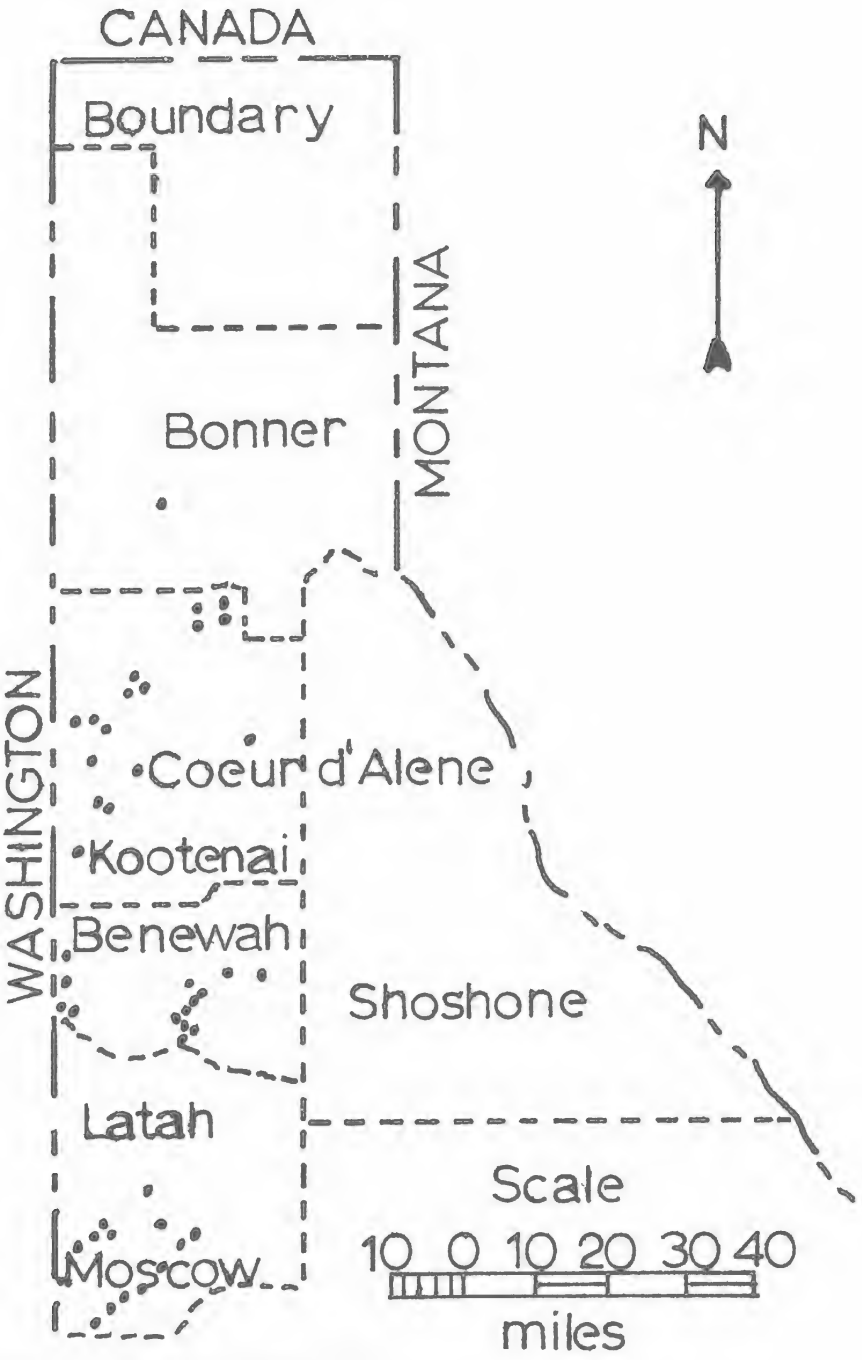

Figure 1. Location of sites used in study.

profiles were described; site conditions, including kind and nature of vegetation, were recorded. Soil Conservation Service soil survey field sheets were used as guides in locating the various soil series.

Soil temperatures were measured on the 15th or 16th of each month with a Weston testing thermometer or a three-pen distant thermograph. Readings were taken with the Weston thermometer at a depth of 20 in by digging a hole with a tile spade or an auger and inserting the thermometer into the soil. Only summer temperatures (June, July, and August) were taken for Shoeffler,[2] Helmer, Huckleberry, and Blossom[2] soils because of inaccessible conditions during the remainder of the year.

An extension soil auger was used to measure temperatures at depth intervals of 20 in to a depth of 20 to 30 ft, depending upon depth of rock or other restrictions. These investigations were attempted at several sites to check the validity of the temperature stability with depth hypothesis (Smith, 1964; Chang, 1958, Vol. I). This hypothesis indicates soil temperatures are stable below 20 to 30 ft, and one reading at these depths will be very close to the mean annual soil temperature.

The Weston thermometer (stem type) Model 2261 is a dial-type thermometer with a temperature range of 25° to 125°F. The thermometer's accuracy, according to factory calibrations, is within 0.50; the thermometer's sensing element is bimetallic. The bimetal thermometer functions on the principle of the different expansion rates of the materials. The two metals in the case of the thermometer are nickel steel alloys. This instrument was used at all sites in addition to the instruments mentioned for specific sites.

The three-pen distant thermograph is equipped with three flexible capillary tubings 6 ft long, with temperature sensing bulbs on the ends. Sensing elements were buried at depths of 6, 20, and 40 inches. Thermograph charts were changed every seven days. The thermograph was used at one Latahco site in addition to the Weston thermometer. Thermograph bulbs and capillary tubing were installed by digging a soil pit and cutting horizontal holes the size of the bulbs in the soil profile. The bulbs were placed in the horizontal incisions with soil packed around the bulb to approximate natural conditions and avoid areas of water accumulation. Capillary tubes were protected from the weather by a box extending from the base of the weather shelter to 6 in into the soil. The tubes were insulated with fiberglass insulating material.

Results and Discussion

Temperatures and other characteristics of some Mollisols in the areas are presented in Table 1. These soils are located in western portions of Benewah and Latah counties. Data from more than one pedon show the range of temperature in the series. Aspect or direction of slope appears to be the important factor regulating soil temperatures in the Mollisols developing in deep loess. The Palouse (south slope) and Thatuna (north slope) sites are approximately 50 ft apart and the mean annual soil temperatures differ by 4° as shown in Figure 2. The temperature difference is explained by two of Baver's (1959) factors that affect solar radiation reception, (1) slope and exposition and (2) nature of the soil and of the vegetation growing on it.

[2] These are tentative soil series and have not been correlated in the national soil classification system.

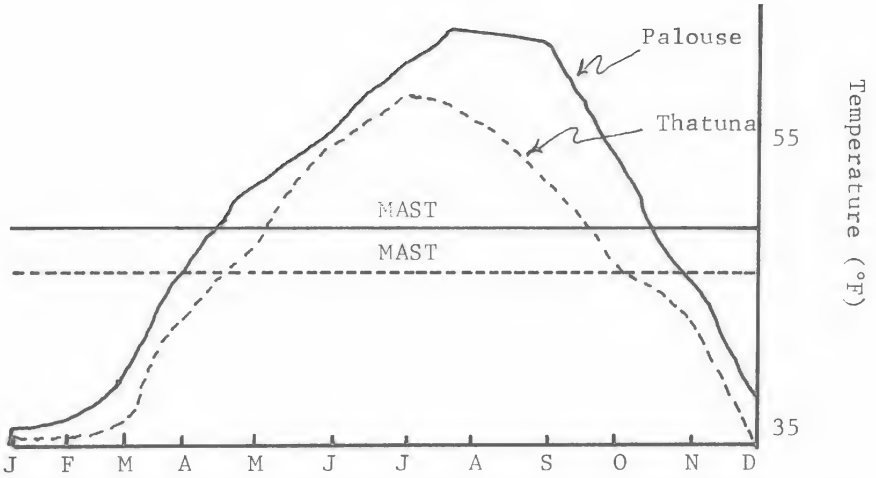

Figure 2. Mean monthly and annual soil temperatures at 20 in deep on Thatuna soil (north slope) and Palouse soil (south slope) near Moscow, Idaho 1966-69.

Variations in temperatures of soils that are both forested and cultivated indicate an influence of the organic surface horizon on the mean annual soil temperatures as shown in Table 2. Character of the soil surface cover has been recognized as an important factor influencing soil temperature (May, 1954; Golovin, 1962; Moody, 1963; Ekern, 1967). Heatly (1967) reported that temperature sites only 6 meters apart showed differences in mean annual soil temperature of 1.7°C (3°F) due to slight variations in ground cover.

The mean annual soil temperatures of the same soil series under cultivated and forested conditions may differ considerably. This is a problem in classifying the soils in most of north Idaho. One principle of the classification system is to keep cultivated soils and similar soils under natural vegetation in the same class until one or more of the diagnostic horizons or features has been significantly and permanently

TABLE 1. Temperatures and other characteristics of Mollisols developed in deep loess or alluvium, 1966-69.

Series	Percent slope	Aspect	Elevation feet	MSST* °F	MAST** °F
Palouse	2	south	2700	62.5	48.8
Palouse	15	south	2640	63.1	49.7
Palouse	level	southeast	2720	60.7	47.8
Latahco	level	bottomland	2642	59.5	47.3
Latahco	level	bottomland	2664	61.4	48.2
Thatuna	12	north	2660	59.0	47.2
Thatuna	30	north	2660	59.8	46.1
Caldwell	level	bottomland	2649	59.3	47.5
Unnamed (99)	8	south	2600	65.2	49.9

* Mean summer soil temperature—average of June, July, and August temperatures.
** Mean annual soil temperature—average of twelve monthly readings.

TABLE 2. Mean annual and summer soil temperatures for cultivated and forested soils of the same series, 1966-69.

Series	Ground cover	Elevation feet	MSST*	MAST**
Kruse+	cultivated	2550	63.7	49.5
	forested	2550	55.3	45.0
Santa	cultivated	2690	58.9	46.7
	forested	2690	50.4	43.8
Taney+	cultivated	2720	62.4	48.2
	forested	2720	53.1	45.4
Southwick	cultivated	2600	60.3	48.4
	forested	2600	52.8	45.9

* Mean summer soil temperature—average of June, July, and August temperatures.
** Mean annual soil temperature—average of twelve monthly readings.
+ These are tentative soil series and have not been correlated in the national soil classification system.

altered (Soil Survey Staff, 1960). Cultivated and forested soils of the same series are classified the same. Organic horizons on soils cause higher monthly soil temperatures in winter and late fall and lower soil temperatures in late spring and summer. The monthly differences between cultivated and forested sites of the same series are large enough to influence the mean annual soil temperatures considerably.

The soils in the study area are deepest in the western portion and become progressively thinner eastward. Therefore, numerous deep borings in various climatic zones were not possible because of depth to bedrock. Coarse fragments and sand in the alluvial bottomlands were limiting factors in deep borings attempted. The successful borings show a close agreement between mean annual soil temperatures based on the average of twelve monthly readings and the soil temperature at the deepest point in the boring as shown in Table 3.

TABLE 3. Variations of soil temperatures with depth.

Depth (ft)	Palouse series June 14, 1967 Temp. °F	Southwick series** June 28, 1967 Temp. °F	Taney series** June 30, 1967 Temp. °F+
5	50.0	51.8	53.6
10	48.2	48.2	48.2
15	48.2	46.4	50.0
20	50.0	51.8	50.0
25	50.0	48.2	50.0
30	50.0	Bedrock	Bedrock
Deepest point °F	50.0	48.2	50.0
MAST*	49.5	48.4	49.3

* The MAST are based on the averages of twelve monthly readings on the 15th of the month at the site of the deep boring.
** Site was on a ridge and was not used as a basis for classification of the series in Table 5.
+ This series is tentative and has not been correlated in the national soil classification system.

Only one three-pen distant thermograph was used in the study; therefore, interpretations or projections are limited relative to the data obtained. The thermograph data at 20 in are summarized in Table 4. The largest variations between the monthly

TABLE 4. Comparison of monthly mean and 15th-of-month reading from thermograph—Latahco series.

Date	Monthly mean—°F	15th-of-month reading—°F*	°F Difference
October 67	57.5	53.6	+3.9
November 67	43.7	46.4	−2.7
December 67	36.9	36.5	+ .4
January 68	34.7	35.6	+ .1
February 68	37.8	37.4	+ .4
March 68	42.8	42.8	——
April 68	43.6	44.6	−1.0
May 68	52.0	53.7	−1.7
June 68	58.6	57.2	+1.4
July 68	63.7	63.5	+ .2
August 68	63.9	63.5	+ .4
September 68	59.0	60.8	−1.8
Annual Average	49.5	49.7	− .2

* Readings taken from thermograph on 15th of month.

means and the 15th-of-the-month readings occurred in the fall and late spring of the year. Reasons for these variations are difficult to explain from these limited data; however, the large variations of diurnal air temperatures possibly influenced the temperature-sensitive lead wires and spring-coiled tube of the thermograph. The head and capillary tubes of the thermograph were subjected to large variations in atmospheric temperatures during these seasons. There is a close agreement between the annual average monthly and the 15th-of-the-month reading. Other atmospheric conditions such as time, duration, and intensity of rain or snow may affect the soil temperature at the 20-in depth, within a 24- or 48-hour period. These factors were not observed or evaluated. More study is needed to support this hypothesis.

Mean summer soil temperature is an important factor in the classification of Shoeffler,[3] Huckleberry, Blossom,[3] and Helmer soils. Mean annual soil temperature was assumed to be less than 47°F. The determination of whether these soils were in the cryic great group was the major question. Therefore, only the mean summer soil temperatures are given for these sites along with the mean annual soil temperature of other sites in Table 5.

Classification of 23 series in Table 5 is based on the 1967 supplement to the Soil Classification System.[4] Where soil temperatures under both forested and cultivated conditions were taken, the temperatures under forested conditions were used in the classification. The soils were classified as Spodosols, Mollisols, Inceptisols and Alfisols.

The classification of some of the series in Table 5 is based on Placement of Series in West Region (Soil Survey Staff, 1968). The temperature data indicate Helmer and Huckleberry soils have summer temperatures too warm for cryic great groups. However, the Huckleberry series is on the temperature class separation line with a mean summer soil temperature of 47°F. The mean annual soil temperature of the Southwick series is just below the temperature class line for mesic soils, and probably should be classified in the frigid temperature class.

[3] These are tentative series and have not been correlated in the national soil classification system.
[4] Unpublished Soil Conservation Service laboratory data were used as an aid in classification.

TABLE 5. Classification of soils in study.

Series	MSST*	MAST*	Classification
29 (unnamed)***	54	44	Loamy-skeletal, mixed, frigid Typic Haploxerolls
71 (unnamed)	56	46	Loamy-skeletal, mixed, frigid Typic Dystrochrepts
Blossom+	45		Coarse-loamy, mixed Typic Cryorthods
Bonner (2)**	52	43	Coarse-loamy, over sandy or sandy-skeletal, mixed, frigid Typic Haplorthods
98 (unnamed)***	66	50	Fine-loamy, mixed, mesic Ultic Argixerolls
Caldwell***	59	46	Fine-silty mixed, frigid Cumulic Haploxerolls
99 (unnamed)***	65	50	Fine-silty, mixed, mesic Calcic Argixerolls
144 (unnamed)	53	45	Coarse-loamy over sandy or sandy-skeletal mixed, frigid Typic Dystrochrepts
Helmer (2)	49		Coarse-silty, mixed Alfic Cryic Fragiorthods
Huckleberry (3)	47		Loamy-skeletal mixed, Typic Cryorthods
Kruse+ (2)	55	45	Fine-loamy, mixed, Typic Eutroboralfs
Larkin***	63	50	Fine-silty, mixed, mesic Ultic Argixerolls
Latahco (2)***	60	46	Fine-silty, mixed, frigid Argiaquic Xeric Argialbolls
Palouse (3)***	63	49	Fine-silty, mixed mesic Pachic Haploxerolls
Porrett+	54	45	Fine-silty, mixed, frigid Typic Fragiaqualfs
715 (unnamed)	52	44	Coarse-silty, mixed, frigid Typic Haplorthods
Santa (3)	50	44	Fine-silty, mixed, frigid Typic Fragiochrepts
Shoeffler+	46		Loamy-skeletal, mixed Typic Cryorthods
Southwick (2)	53	46	Fine-silty, mixed, mesic Boralific Argixerolls
Taney+ (3)	53	45	Fine-silty, mixed, frigid Glossoboralfic Paleborolls
Thatuna (2)	60	46	Fine-silty, mixed, frigid Boralfic Argixerolls
Ulricher+	60	50	Coarse-loamy, mixed, mesic Typic Dystrochrepts
Vassar (4)	50	44	Coarse-loamy, mixed, frigid Typic Haplorthods

* Temperatures rounded off to the nearest degree.
** Number of sites of soil series used in study.
*** Series cultivated; other series have thin 0 horizons.
+ These are tentative series and have not been correlated in the national soil classification system.

Conclusions

Thickness of surface organic horizons profoundly affects both mean annual and summer soil temperatures. Therefore, the definition of a surface organic horizon as used in the classification system should be revised to include specific thickness requirements. It appears that an organic horizon of 1.5 to 2 in may significantly affect mean annual soil temperatures in the three north Idaho counties.

Deep borings, when practical in Latah, Benewah, and Kootenai counties, appear adequate for the determination of mean annual soil temperatures for soil classification.

The Model 2261 Weston thermometer appears adequate for mean annual soil temperature determinations, based on averages of periodic observations. Its major disadvantages are: (1) it provides no information relative to maximum and minimum conditions, and (2) it lacks the continuous records provided by thermographs. The instrument does not require an installation, and this increases its desirability for use in measuring temperatures in cultivated fields.

Literature Cited

Baver, L. D. 1959. Soil temperatures, p. 288-310. In L. D. Baver, Soil physics. John Wiley and Son, New York.

Chang, Jen-Hu. 1958. Ground temperature, Vol. I. Blue Hill Meteorological Observatory, Harvard University, Milton, Mass. 300 pp.

Ekern, P. F. 1967. Soil moisture and temperature changes with the use of block vapor barrier mulch and their influence on pineapple growth in Hawaii. Soil Sci. Soc. Amer. Proc. 31: 270-275.

Golovin, V. V. 1962. Description of the temperature regime of soils in the Amur region. Translated in Soviet Soil Science, same issue date, p. 213-217, by Scripta Technical, Inc., 1963.

Heatly, I. N. 1967. Ecological study of temperature in a Welsh moorland soil, 1962-63. J. Animal Ecology 36: 425-434.

May, M. 1954. Some effects of mulches on soil temperature in the Bighorn Mtns. M.S. thesis. University of Wyoming, Laramie.

Moody, J. E. 1963. Influence of straw mulch on soil moisture, soil temperature and growth of corn. Soil Sci. Soc. Am. Proc. 27: 700-703.

Moore, Elbert. 1969. Temperatures and classification of soils in Latah and Benewah Counties, Idaho. M.S. thesis. University of Idaho, Moscow.

Smith, G., D. F. Newhall, L. H. Robison, and D. Swanson. 1964. Soil temperature regimes —their characteristics and predictability. USDA Soil Conservation Service Technical Paper 144. 14 p.

Soil Survey Staff. 1960. Soil Classification, a comprehensive system, 7th approximation. U.S. Gov't. Printing Office, Washington, D.C. 265 p.

Soil Survey Staff. 1967. Supplement to soil classification system, dated March 24, 1967. 218 p.

Soil Survey Staff. 1968. Placement of Series West Region, dated July 1968. USDA-SCS. Portland, Oregon.

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Note on the Occurrence of Dribblet Spires in the Snake River Plain, Idaho

The volcanic nature of parts of the lunar mare, confirmed by Apollo samples, has prompted interest in volcanic landforms, particularly those associated with basalt lava flows. During an investigation of lava tubes and channels in the Snake River Plain, Idaho, several *dribblet spires* (heretofore unreported in the continental United States) were found on the Wapi Lava Field (Fig. 1). Although similar to hornitos in origin, dribblet spires are distinctive features which may be common in some basalt flows.

Stearns (1966) described dribblet spires in Hawaii and illustrated a well-known spire (named Madame Pele after its fancied resemblance to a standing female figure). He attributed dribblet spires, ranging in size from a few feet to more than 16 ft. high, to accretion of lava clots feebly ejected from small holes in the crust of an active flow. Hornitos and spiracles, in contrast, form by the ejection of material from cracks over lava tubes, are irregular in form, and may be much larger than dribblet spires.

The Wapi Lava Field is a Holocene basalt flow of predominantly pahoehoe lava related to the Idaho Rift System (Prinz, 1970). Pillar Butte, a major vent in the north part of the flow, marks the last eruptive stage of the Wapi field and is characterized by lava tubes, channels, collapse structures, and thin sheets of slab and shelly pahoehoe. At least three dribblet spires (Fig. 2) occur on the flows of Pillar Butte. The spires appear to be solid and average 12 ft. in height and about 5 ft. in diameter. There is no indication that the spires formed over a lava tube, nor are there vents near the structures. Apparently, pasty lava was extruded from a small circular vent in the crust of the active flow, like toothpaste from a tube, with clots of lava pushing the structure vertically from below. The dribblet spire consists of imbricating, rounded slabs of lava. Slabs range in size from 5 inches by 5 inches by 1 inch thick to 12 inches by 9 inches by 4 inches thick. Although much of the Pillar Butte Flow was examined during a two-week period, no structures were found which could be described as dribblet spires that might have toppled during, or after, their formation. This is rather surprising in view of the probable mode of formation, and an explanation is lacking.

Although this is the first known report of dribblet spires in the United States outside Hawaii, these structures may be expected to be found in young basaltic pahoehoe flows.

Resolution of most lunar photographs at present does not permit discrimination of features on the moon the size of dribblet spires. It is probable that most lunar

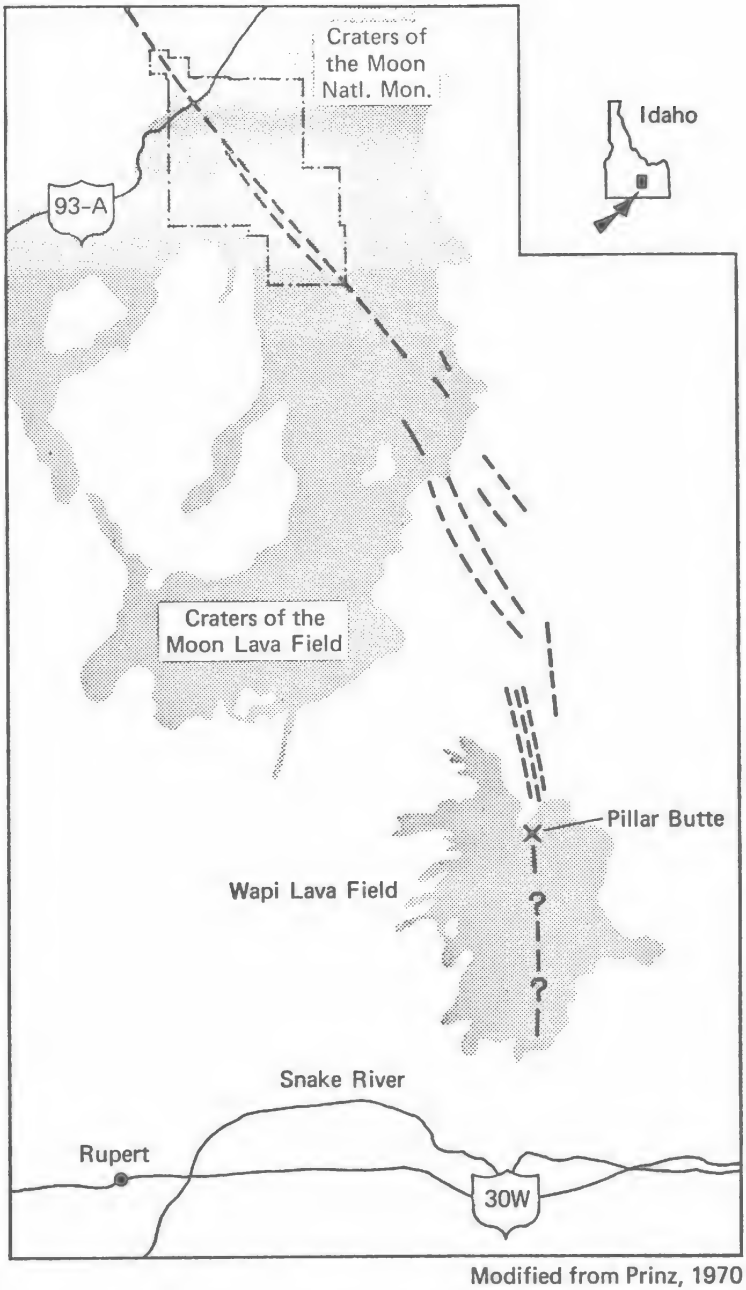

Figure 1. Location of Wapi Lava Field and Pillar Butte eruptive vent in the Snake River Plain, Idaho. Dashed line shows the approximate position of the Idaho Rift System. Map modified from Prinz (1970).

Figure 2. Dribblet spire on Pillar Butte Flow, showing typical imbricating slabs of pahoehoe lava. Half-gallon canteen at base indicates scale.

dribblet spires would have been eroded, possibly beyond recognition, in consideration of the great age of lunar mare surfaces (3.3 billion years, compared to less than 1 million years for the Wapi Lava Field). Lunar areas such as the Marius Hills

(Karlstrom *et al.,* 1968), however, and parts of the crater Copernicus, which are suspected as being relatively young and basaltic, may have remnants of dribblet spires on their surfaces.

I wish to acknowledge J. Papadakis of American Falls, Idaho, who referred me to Stearn's (1966) work and to thank M. Lovas for his able assistance during field studies in the Snake River Plain. This work was conducted during tenure as a NASA-National Academy of Sciences Associate.

Literature Cited

Karlstrom, T. N. V., J. F. McCauley, and G. A. Swann, 1968. Preliminary lunar exploration plan of the Marius Hills Region of the Moon. Astrogeology 5, U.S. Geological Survey open-file report, 42 p.

Prinz, M., 1970. Idaho Rift System, Snake River Plain, Idaho. Geol. Soc. America Bulletin 81: 941-948.

Stearns, H. T., 1966. Geology of the State of Hawaii. Pacific Book, Palo Alto, Calif., 266 p.

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Interaction of Ca^{++} and Mg^{++} in Regulation of Electrophysiological Properties of Frog Twitch Muscle Membrane

Present understanding of the electrophysiology of the skeletal muscle membrane derives mostly from experiments which have been performed on the isolated sartorius muscle of the frog. Advances in electronic instrumentation and the development of the microelectrode technique for intracellular recording have permitted the accumulation of a considerable body of quantitative information during the past 20 years. The sartorius muscle has been widely used because of its relative ease of dissection, because it is thin and pale and hence may be transilluminated for direct visualization of microelectrode impalements, and because it will maintain its electrical excitability for long periods of time *in vitro* (Levine, 1966).

Currently the features of electrical excitability are interpreted in terms of ionic mechanisms. Therefore, if properties measured *in vitro* are to describe the normal *in vivo* situation, it is necessary to suspend the isolated preparation in a solution which duplicates the interstitial fluid of the frog. Such solutions are usually referred to as Ringer's solutions and they are prepared from data derived from analysis of frog plasma. (To be more accurate, the plasma concentrations of the ionic constituents would have to be corrected for the Donnan factor operating across the capillary membrane.)

Most of the frog Ringer's solutions in use are based on the data given by Fenn (1936). These data, confirmed by others (Conway, 1957), show that one of the normal constituents of frog plasma is Mg, which occurs at a concentration of 1-3 mM. It is therefore surprising that almost every electrophysiological study which has been performed on the isolated frog sartorius muscle has been conducted in an Mg-free Ringer's solution.

Figure 1 lists eight papers which have contributed significantly to our understanding of the electrical excitability of the skeletal muscle membrane within the last 20 years. All of the studies enumerated are well designed, carefully controlled and conducted, employ advanced electronic technology, use microelectrode techniques, and make use of the isolated frog sartorius muscle. The additional feature which all of these studies share is that they make use of a Ringer's solution which contains no Mg. Now it is well known that both Mg and Ca ions influence a number of membrane processes, and that the effects are in some cases synergistic and in some cases antagonistic (Engbaek, 1952). Therefore the present study was undertaken primarily to answer the question of whether existing electrophysiological data for the frog sartorius muscle, obtained in Mg-free media, provide an accurate quantitative description of the normal fiber membrane *in vivo*. Some of these results have been briefly reported (Levine, 1970).

LING, G. AND R. W. GERARD 1949 THE NORMAL MEMBRANE POTENTIAL OF FROG SARTORIUS FIBERS. J. CELLULAR COMP. PHYSIOL. 34:383.

NASTUK, W. L. AND A. L. HODGKIN 1950 THE ELECTRICAL ACTIVITY OF SINGLE MUSCLE FIBERS. J. CELLULAR COMP. PHYSIOL. 35:39.

FATT, P. AND B. KATZ 1951 AN ANALYSIS OF THE END-PLATE POTENTIAL RECORDED WITH AN INTRA-CELLULAR ELECTRODE. J. PHYSIOL. 115:320.

ADRIAN, R. H. 1956 THE EFFECT OF INTERNAL AND EXTERNAL POTASSIUM CONCENTRATION ON THE MEMBRANE POTENTIAL OF FROG MUSCLE. J. PHYSIOL., LONDON 133:631.

HODGKIN, A. L. AND P. HOROWICZ 1959 THE INFLUENCE OF POTASSIUM AND CHLORIDE IONS ON THE MEMBRANE POTENTIAL OF SINGLE MUSCLE FIBRES. J. PHYSIOL., LONDON 148:127.

JENERICK, H. 1963 PHASE PLANE TRAJECTORIES OF THE MUSCLE SPIKE POTENTIAL. BIOPHYS. J. 3:363.

LEVINE, L. 1966 THE EFFECTS OF MODIFIED RINGER'S SOLUTIONS ON THE MEMBRANE POTENTIALS OF INNERVATED AND DENERVATED FROG SARTORIUS MUSCLE FIBERS. J. CELLULAR PHYSIOL. 67:107.

GAGE, P. W. AND R. S. EISENBERG 1969 ACTION POTENTIALS, AFTERPOTENTIALS, AND EXCITATION-CONTRACTION COUPLING IN FROG SARTORIUS FIBERS WITHOUT TRANSVERSE TUBULES. J. GEN. PHYSIOL. 53:298.

Figure 1. Eight significant electrophysiological studies published since the introduction of microelectrode techniques, dealing with the frog sartorius muscle. All of these studies were conducted in Ringer's solutions containing no Mg ions.

Methods

All investigations were performed on sartorius muscles which were carefully dissected from *Rana pipiens* and mounted in a water-jacketed muscle chamber containing Ringer's solution buffered to pH 7.25, with temperature thermostatically regulated to 20°C $\pm$ 0.7°C. The composition of the complete Ringer's solution was (in mM): NaCl—115; KCl—2.5; $CaCl_2$—1.8; $MgSO_4$—1.2; NaH_2PO_4—0.85; Na_2HPO_4—3.98. Conventional microelectrode techniques were used to impale individual muscle fibers (Levine, 1966a). Glass micropipettes were freshly drawn and filled with 3M KCl on the day of the experiment, and selected for relatively low resistance (7-12 MΩ) and tip potentials $<$ 5 mV, as previously described (Levine, 1966b). The microelectrode was connected to a solid state "negative capacitance" electrometer containing a field-effect transistor input. Leakage current was adjusted to $< 10^{-12}$ A. Prior to each impalement, the input time constant was compensated to $<$ 20 μsec. An external stainless steel electrode, insulated except for its 50μ tip, was used to stimulate directly the impaled fiber ca. 3 mm from the recording site. The resulting action potential, recorded on a dual beam oscilloscope, was displayed in the usual way (V, t) on one channel, and simultaneously in the "phase plane" (V, dV/dt) on the other channel. In this latter case the action potential was fed into an operational amplifier connected as a differentiating circuit. The output signal, dV/dt, was used to drive the horizontal deflection circuit of the second channel of the oscilloscope. The vertical axis recorded voltage and was common to both channels. There are a number of important practical and theoretical advantages to this method of recording (Jenerick, 1963, 1964).

Figure 2 shows a typical phase plane registration of the action potential. Line A—A is the baseline for the voltage measurements made vertically, and line B—B

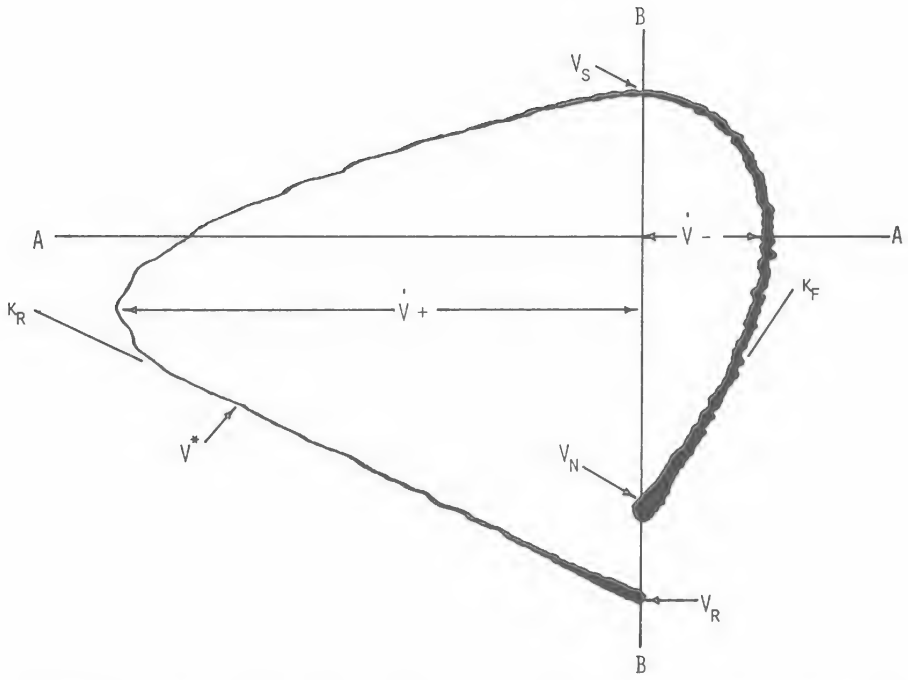

Figure 2. Example of phase plane recording of the action potential of a single frog sartorius muscle fiber. The membrane voltage is recorded vertically and the first-time derivative of this voltage is registered horizontally. The various features of the action potential which were measured are indicated by symbols which are explained in the text. This recording was made with the high frequency response of the system limited to 3 KHz, in order to minimize electrical noise on the trace. Actual recordings analyzed were obtained with a high frequency response extending to 10 KHz, and also contained the action potential displayed as a function of time on a second channel.

is the baseline for the dV/dt measurements made horizontally. The 10 electrophysiological properties studied are identified. These were (following Jenerick, 1963):

V_r—resting potential

V_s—spike amplitude (measured from resting potential)

V_{amp}—active membrane potential (measured from zero potential baseline)

$\dot{V}+$—maximum rate of rise of spike

$\dot{V}-$—maximum rate of fall of spike

k_r—rate constant of foot of action potential

k_f—rate constant of terminal part of spike

V_n—negative afterpotential (measured from zero potential baseline)

V'_n—negative afterpotential (measured from resting potential)

V^*—excitation voltage (measured from zero potential baseline to point where phase plane tracing first departs from linearity)

In each experiment the sartorius muscle was dissected and the preparation allowed to equilibrate for 60 min in Ringer's solution containing 1.2mM Mg. A sample of 14-20 fibers was measured, then the bath was drained and the preparation washed several times with Mg-free Ringer's solution. After a 30-min equilibration, a second sample of 14-20 fibers was measured. The bath was again drained, the preparation

washed several times with Ringer's solution containing 1.2mM Mg and, after a 30-min equilibration, a final sample of 14-20 fibers was measured.

For each sample of 14-20 fibers the mean and standard errors were calculated for each of the ten electrophysiological properties measured. The differences between these means in the two solutions were tested for statistical significance using Student's t-test. In calculating the means in Mg-containing Ringer's solution, the measurements made before and after exposure to the Mg-free medium were combined. This series involved five different muscles, which included a total of 248 determinations for each of the ten properties studied. The mean difference for each of the properties in the five muscles in this series was also calculated, and this mean difference was tested to see if it differed significantly from zero. In practice, both of these statistical approaches yielded the same result.

Results and Discussion

Table 1 summarizes the results by showing the mean values found in the Ringer's solution containing Mg and in the Mg-free solution. None of the properties studied

TABLE 1. Effect of addition of magnesium ions to Ringer's solution on electrophysiological properties of sartorius muscle fibers of *Rana pipiens*.

CONC (mM)		V_R	V_{AMP}	V_S	$\dot{V}+$	$\dot{V}-$	k_R	k_F	V_N	V_N^4	V^*
Ca	Mg	mV	mV	mV	V/SEC	V/SEC	$MSEC^{-1}$	$MSEC^{-1}$	mV	mV	mV
1.8	0.0	–89.7	38.4	130	519	116	7.93	2.40	–80.3	11.1	–39.3
		±0.7	±0.7	±1	±10	±2	±0.16	±0.05	±0.6	±0.7	±1.0
1.8	1.2	–90.9	38.8	130	501	116	7.51	2.40	–79.1	11.8	–37.1
		±0.7	±0.6	±1	±10	±1	±0.17	±0.05	±0.5	±0.6	±0.9

Values represent mean of five muscles ± mean standard error. For 1.8mM Ca + 0mM Mg number of determinations was 98; for 1.8mM Ca + 1.2mM Mg number of determinations was 150.

differed in a statistically significant way when Mg ions were excluded from the Ringer's solution. From this it would appear that the electrophysiological properties of frog sartorius muscle fibers, at least those examined in this study, are not altered quantitatively by omitting Mg ions from the Ringer's solution.

This result raised the possibility that Mg ions have no influence on the electrophysiological properties of frog muscle. This conclusion, however, is not consistent with results of other studies on nerve (Frankenhaeuser and Hodgkin, 1957; Frankenhaeuser and Meves, 1958). An alternative possibility is that the processes which are affected by Ca ions are affected synergistically by Mg ions, but these processes are saturated by the normal concentration of Ca ions. To test this possibility, experiments were conducted to determine whether Mg ions could substitute for Ca ions in Ringer's solution. These experiments were performed in a manner similar to the previous ones, using Ringer's solutions which contained 1.8mM Ca but no Mg, and then 1.2mM Mg but no Ca.

The results of these experiments are summarized in Table 2, which indicates that when only Mg ions are present, the electrophysiological properties are maintained at essentially normal values, suggesting that Mg ions may substitute for Ca ions in those processes which determine electrical excitability. In the case of three of the properties, the values in the Ringer's solution in which Mg was substituted for Ca differed in

TABLE 2. Effect of substituting magnesium ions for calcium ions in Ringer's solution on electrophysiological properties of sartorius muscle fibers of *Rana pipiens*.

CONC (mM) Ca	Mg	V_R mV	V_{AMP} mV	V_S mV	$\dot{V}+$ V/SEC	$\dot{V}-$ V/SEC	k_R MSEC^{-1}	k_F MSEC^{-1}	V_N mV	V^1_N mV	V^* mV
1.8	0.0	–92.9	41.6	135	567	120	8.25	2.35	–79.0	14.0	–35.9
		±0.7	±0.7	±1	±8	±2	±0.16	±0.05	±0.8	±0.9	±0.2
0.0	1.2	–91.1	41.5	133	619[1]	122	9.85[1]	2.32	–79.3	11.9	–41.5[1]
		±0.6	±0.7	±1	±11	±2	±0.19	±0.05	±0.7	±0.8	±0.7

Values represent mean of two muscles ± mean standard error. For 1.8mM Ca + 0.0mM Mg number of determinations was 57; for 0.0 mM Ca + 1.2 mM Mg number of determinations was 31.
[1] Value differs in statistically significant way ($P < 0.01$) from value in Ringer's solution containing 1.8mM Ca + 0.0mM Mg.

a statistically significant way from the values recorded in Mg-free Ringer's solution. The maximum rate of rise ($\dot{V}+$), the rate constant for the foot of the action potential (k_r), and the excitation voltage (V^*) were not fully restored to the levels observed when Ca was present. This may mean that Mg ions are not as effective as Ca in controlling these properties, and that the Mg concentration normally occurring in frog plasma is insufficient fully to saturate these mechanisms. The more important conclusion, however, is that the electrically excitable system of frog muscle membrane is preserved at essentially normal levels by the concentration of Mg ions found in frog plasma, when only trace amounts of Ca ions are present.

Further to explore the idea that Ca ions, at the concentration at which they normally occur in frog plasma, fully saturate the processes underlying electrical excitability, additional experiments were performed on muscles suspended in Ringer's solutions with reduced Ca ion concentration. The results of these studies are summarized in Table 3. The same three properties which were altered in the Ca-free

TABLE 3. Effect of reduction of calcium ion concentration in Ringer's solution on the electrophysiological properties of sartorius muscle fibers of *Rana pipiens*.

Ca CONC (mM)	V_R mV	V_{AMP} mV	V_S mV	$\dot{V}+$ V/SEC	$\dot{V}-$ V/SEC	k_R MSEC^{-1}	k_F MSEC^{-1}	V_N mV	V^1_N mV	V^* mV
1.8	–92.8	33.5	125	462	120	9.29	2.57	–77.9	14.8	–52.4
	±0.7	±0.9	±1	±8	±2	±0.15	±0.04	±0.5	±0.7	±1.1
0.18	–88.0[1]	34.6	123	497[1]	122	11.58[1]	2.55	–76.4	11.6[1]	–57.0[1]
	±0.6	±0.6	±1	±7	±2	±0.02	±0.05	±0.5	±0.6	±1.6

Values represent the mean ± standard error for one muscle. For 1.8mM Ca the number of determinations was 29; for 0.18mM Ca the number of determinations was 14.
[1] Value differs in statistically significant manner ($P < 0.01$) from value in Ringer's solution containing 1.8mM Ca.

Ringer's solution containing 1.2mM Mg were affected in the same way when the Ca concentration was reduced to 10 percent of normal in Mg-free Ringer's solution. Thus $\dot{V}+$ and k_r were larger, and V^* occurred at a more negative potential. Two other properties were also different: the resting potential, V_r, was less negative and the negative after potential, V^1_n, was smaller. The reduction of V_r when Ca concentration is lowered has been previously described for frog muscle (Bülbring, Holman, and Lüllmann, 1956), and this change in the resting potential provides an adequate explanation for the reduction in V^1_n. Thus the observations that the same three electrophysiological properties are affected in the same way by lowering Ca concentration as when Mg

ions are substituted for Ca ions lend support to the hypothesis that Ca ions normally occur at a concentration which fully saturates the mechanisms controlling these electrophysiological properties.

If this interpretation is correct, one would predict that addition of 1.2mM Mg to Ringer's solution containing only 10 percent Ca would restore these altered properties toward the values which they possess in Ringer's solution containing 100 percent Ca. Table 4 shows the results of experiments designed to test this. All of the

TABLE 4. Effect of addition of magnesium ions to a Ringer's solution containing 10 percent calcium on the electrophysiological properties of sartorius muscle fibers of *Rana pipiens*.

CONC (mM) Ca	Mg	V_R mV	V_{AMP} mV	V_S mV	$\dot{V}+$ V/SEC	$\dot{V}-$ V/SEC	k_R MSEC^{-1}	k_F MSEC^{-1}	V_N mV	V^1_N mV	V^* mV
0.18	0.0	−88.2	35.8	124	478	107	10.65	2.39	−76.2	12.8	−46.7
		±0.7	±0.9	±1	±11	±2	±0.19	±0.05	±1.0	±1.0	±0.8
0.18	1.2	−91.3[1]	37.6	125	449[2]	103	9.51[1]	2.37	−74.1	17.2[1]	−40.3[1]
		±0.8	±0.7	±1	±9	±2	±0.17	±0.05	±0.7	±0.8	±1.0

Values represent the mean of two muscles ± mean standard error. For 0.18mM Ca + 0.0 mM Mg the number of determinations was 35; for 0.0mM Ca + 1.2mM Mg the number of determinations was 33.

[1] Value differs in statistically significant way ($P < 0.01$) from value in Ringer's solution containing 0.18mM Ca + 0.0mM Mg.

[2] Value differs with borderline statistical significance ($P \simeq 0.05$) from value in Ringer's solution containing 0.18mM Ca + 0.0mM Mg.

properties in question, *viz.*, V_r, $\dot{V}+$, k_r, V^1_n, and V^*, are changed when Mg ions are added to the Ca-deficient Ringer's solution. Further, these changes are all in the directions required and are statistically significant ($P < 0.01$) for V_r, k_r, V^1_n, and V^*, and of borderline significance ($P \simeq 0.05$) in the case of $\dot{V}+$.

Summary

Ten electrophysiological properties are not changed in value when Mg ions are included in the Ringer's solution in which the isolated frog sartorius muscle is maintained. If Ca ions are excluded from Ringer's solution, Mg ions are able to substitute and to preserve the electrophysiological properties at essentially normal levels. The hypothesis seems tenable that the concentration at which Ca ions normally exist in the interstitial fluid of frog sartorius muscle fully saturates those processes which underlie electrical excitability.

Acknowledgement

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Literature Cited

Bülbring, E., M. Holman, and H. Lüllmann. 1956. Effects of calcium deficiency on striated muscle of the frog. J. Physiol. 133: 101-117.

Conway, E. J. 1957. Nature and significance of concentration relations of potassium and sodium ions in skeletal muscle. Physiol. Rev. 37: 84-132.

Engbaek, L. 1952. The pharmacological actions of magnesium ions with particular reference to the neuromuscular and cardiovascular system. Pharmacol. Rev. 3: 396-414.

Fenn, W. O. 1936. Electrolytes in muscle. Physiol. Rev. 16: 450-487.

Frankenhaeuser, B., and A. L. Hodgkin. 1957. The action of calcium on the electrical properties of squid axons. J. Physiol. 137: 218-244.

————, and H. Meves. 1958. The effect of magnesium and calcium on the frog myelinated nerve fibre. J. Physiol. 142: 360-365.
Jenerick, H. 1963. Phase plane trajectories of the muscle spike potential. Biophys. J. 3: 363-377.
————. 1964. An analysis of the striated muscle fiber action current. Biophys. J. 4: 77-91.
Levine, L. 1966a. The effects of modified Ringer's solutions on the membrane potentials of innervated and denervated frog sartorius muscle fibers. J. Cellular Physiol. 67: 107-123.
————. 1966b. Tip potentials in microelectrodes filled by boiling under reduced pressure. Experientia 22: 559-560.
————. 1970. Magnesium ions and electrical excitability of twitch muscle membrane. Northwest Sci. 44: 64-65.

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The Toad Genus Bufo in Montana

Montana, with its varied physiography, climatic, glacial, and vegetational history, presents a large number of herpetological problems concerning the family Bufonidae. The purpose of this paper is to discuss the distributional patterns and history of the toad genus *Bufo* in Montana. Distribution maps are based on collection records, observation of habitat, and the present physiographic and vegetational patterns.

According to Stebbins (1966) and Conant (1958), there are four toad species in Montana: *Bufo hemiophrys* in northeastern Montana, *Bufo boreas boreas* in western Montana, *Bufo cognatus* in eastern Montana, and *Bufo woodhousei woodhousei* in the southern half of Montana. *B. hemiophrys* was not definitely collected in Montana until 1966 (Black and Bragg, 1968). Black (1967, 1970a, 1971) discussed some aspects of the natural history and distribution of members of these four species in Montana.

Distribution

Montana can be divided into two regions based on vegetation and physiography (Black, 1969). The intermontane region, including much of the western third, is dominated by forests and mountains, while the plains region, including the eastern two-thirds, is dominated by grassland with a few isolated mountain ranges.

The Boreal Toad (*Bufo boreas boreas*) is the most frequently observed in western Montana. It is found throughout the mountainous and forested areas which make up the western third of Montana, and on some of the isolated low mountain groups in central Montana (Fig. 1). It is the common toad in Glacier National Park.

The range of the Great Plains Toad (*Bufo cognatus*) in Montana covers the eastern half of the state in the plains region (Fig. 2). It inhabits the short grass prairie of counties within its range.

The Dakota Toad (*Bufo hemiophrys*) is found in northern Montana (Fig. 3). Its range lies within the area formerly covered with the Laurentide Ice Sheet.

The range of the Rocky Mountain Toad (*Bufo woodhousei woodhousei*) in Montana lies east and south of the Continental Divide (Fig. 4). This is probably the most versatile and wide ranging of Montana toads in its distribution.

During 1966 and 1967, 19 specimens of *Bufo* were collected at Logan Pass and Granite Park, Glacier National Park, Montana. All differed in external characteristics from the typical Boreal Toad. The Glacier National Park collection also contains two of these unusual toads from other localities within the Park. The specimens are most similar to *Bufo canorus* Camp which has been reported only above 6000 to over 11,000 ft of elevation in the central Sierra Nevada of California. *B. b. boreas*

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from other high elevations within Montana show no tendencies toward approaching the structure or coloration of *B. canorus* as do these from certain localities in Glacier National Park. I suggested (Black, 1970b) that the *canorus*-like form of *B. b. boreas* might be a Pleistocene isolate of an ancestral *boreas*-like toad which became isolated in or near its present range in Glacier National Park. The *canorus*-like forms should presently be considered as *B. b. boreas.*

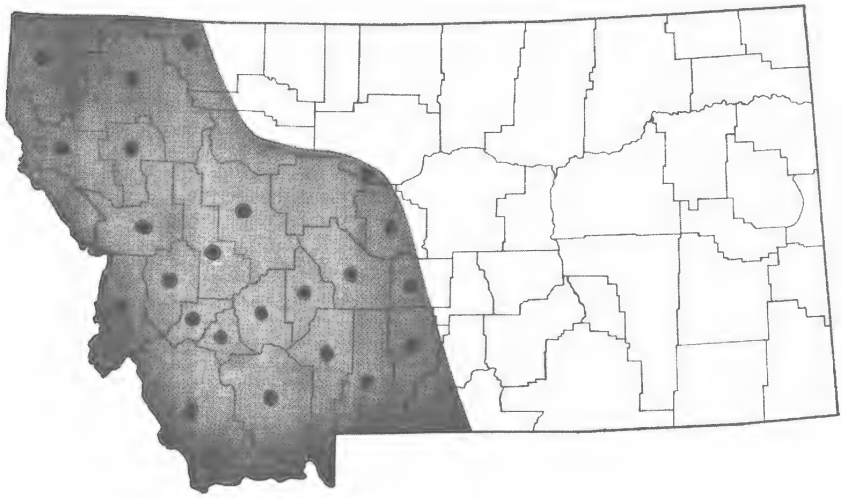

Figure 1. Shaded area shows the general range of *B. b. boreas* in Montana. A black dot indicates a county where this subspecies has been collected.

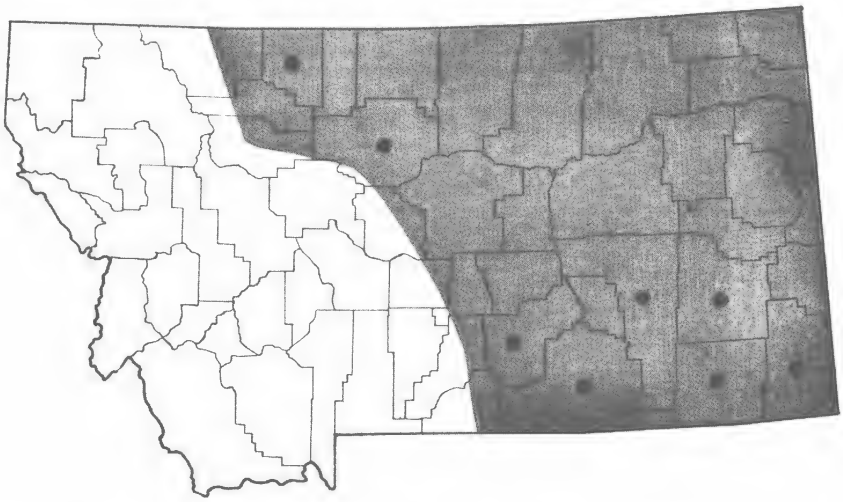

Figure 2. Shaded area shows the general range of *B. cognatus* in Montana. A black dot indicates a county where this species has been collected.

Discussion

The history of bufonids in Montana may be reconstructed as follows. According to Alden (1932, 1953), Flint (1957), and Antevs (1948) the latest glaciation in North America is represented by the classical Wisconsin drift in the central region and by a correlative drift in the Cordilleran region which was laid down in the Pleistocene. The Cordilleran Glacier Complex was a network of glaciers which occupied the mountains of western North America. The drift formed by the Laurentide Ice Sheet

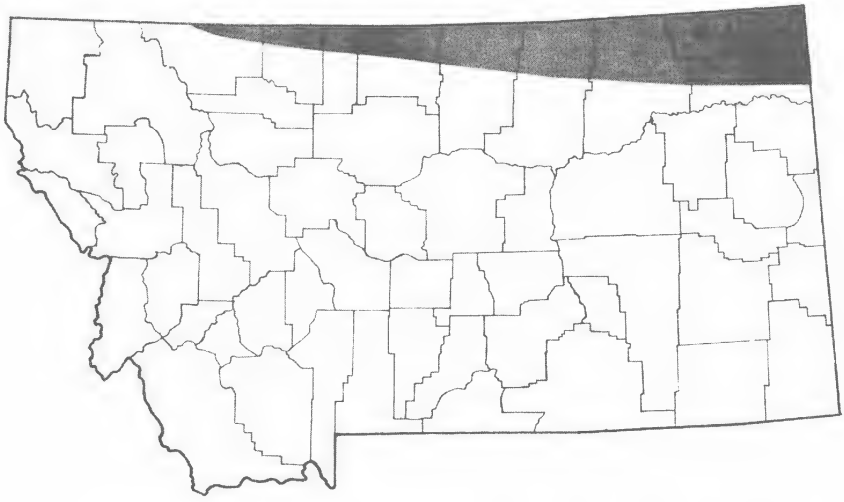

Figure 3. Shaded area shows the general range of *B. hemiophrys* in Montana. A black dot indicates a county where this species has been collected.

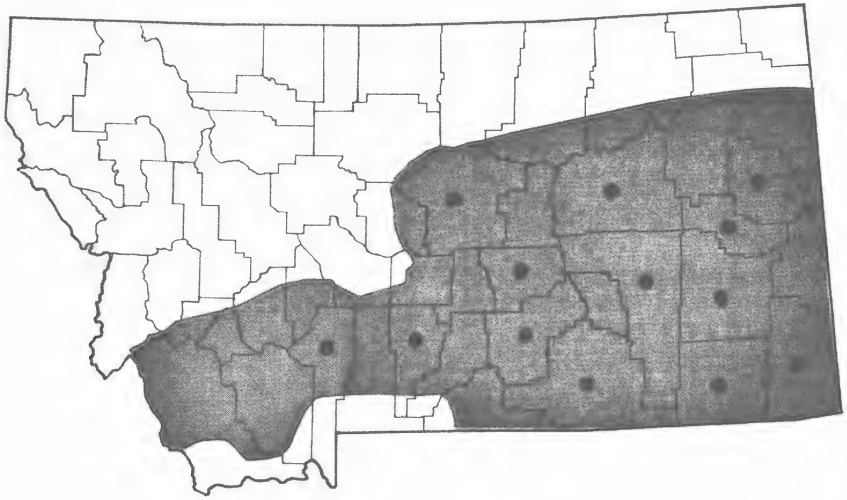

Figure 4. Shaded area shows the general range of *B. w. woodhousei* in Montana. A black dot indicates a county where this species has been collected.

is spread over North America from Newfoundland to the Rocky Mountains. The drift formed by the Cordilleran Glacier Complex occurs on the eastern slope of the Rocky Mountains where the glaciers coalesced at some points with the Laurentide Ice Sheet.

During the Wisconsin and earlier stages of the Pleistocene in Montana there was probably an extensive ice cap covering most of the Yellowstone Park plateau and the Absaroka Range and the Beartooth Mountains to the north and northeast. Farther north, northwest, and west in the region between Yellowstone Park, the Idaho-Montana border, and the Canadian border there were many local glaciers. Some of these glaciers were very large and were headed on the upper slopes of the highest mountain ranges both east and west of the Rocky Mountain front. None, however, advanced far from its source.

In the interior of Glacier National Park several features of possible biogeographic importance are found. A high level sloping bench occurs above the Glacier Wall between Heavens Peak to the west and the big bend on McDonald Creek. Another known as Granite Park is located between the McDonald Creek Valley and the rugged mountain crest north and south of Swiftcurrent Pass. The elevation of these smooth, high-level benchlands is between 6500 and 7000 ft. Another, an interstream and interlake ridge, is in the western part of the broad trough drained by the Flathead River. The fact that these three ridges are well preserved today is probably due to their having been somewhat protected from stream and glacial erosion by their positions between the valley of the North Fork of the Flathead River and that of McDonald Creek where the main glaciation occurred, or between the latter and the Continental Divide of the Rocky Mountain front where the greatest water erosion occurs today.

These three ridges could have remained unglaciated during the Wisconsin time even though they might have carried a persistent snowcap. They could have acted as refugia for animals and plants, and the surrounding glaciers acted as barriers to gene flow.

In eastern Montana during the Pleistocene the Laurentide Ice Sheet of the Wisconsin stage of glaciation advanced into Montana from the northeast and diverted the Missouri River from the north to the south side of the Bearpaw and Little Rocky Mountains. This ice sheet reached the mountains just north of the eastern edge of Glacier National Park and extended southwestward nearly to Great Falls where it also diverted the Missouri River.

On the eastern edge of Glacier National Park there was a glacier in the St. Mary's valley. Here there is a ridge on the west side of Lower St. Mary Lake which is broad and smooth. There is no indication of the upper limit reached by the St. Mary Glacier on this ridge. A bench, nearly 1500 ft above Swiftcurrent Creek on the south and 800 ft above the South Fork of Kennedy Creek on the north, appears to be nonglaciated and could have also acted as a refuge. At the Wisconsin glacial maximum the Laurentide and Piedmont glaciers and permanent snow probably covered most of western Montana and the area north of the Missouri River in eastern Montana.

During the Pleistocene the Boreal Toad, *B. b. boreas,* must have been associated with the short thermal summer conditions found along the Piedmont and Continental glacial margins in western Montana and perhaps those east of the Rocky Mountain front. This toad could have survived the Pleistocene glaciation around the margins

of glacial Lake Missoula west of the Rocky Mountains. Dr. Philip C. Dumas, Central Washington State College, Ellensburg, Washington, has suggested a general hypothesis which he found probably holds true for *Rana pipiens* and *B. woodhousei* in Washington, Oregon, and Idaho. This hypothesis suggests that the longer a frog or toad has been in a particular area, the farther it has invaded the surrounding mountain ranges. He suggested that this hypothesis should be limited to problems of direction of migration or migration routes; that one needs to know that the species is capable of existing at higher altitudes than are now obtained in the general region; and to know that lack of time for spread is the cause of nonoccupancy and not some other limiting factor.

The Boreal Toad has been collected at recorded elevation of over 9500 ft northwest of Dillon in Beaverhead County which is east and south of the Rocky Mountains. West of the Rocky Mountains in western Montana, this species has only been collected up to elevations of 7200 ft in Sanders County with most collection records from elevations of 3000 to 5000 ft. Overgeneralizing with Dumas' thesis, this might indicate that the Boreal Toad has occupied the area east and south of the Rocky Mountains for a longer period of time and reinvaded western Montana through east-central Idaho.

The Rocky Mountain Toad, *B. w. woodhousei,* and the Great Plains Toad, *B. cognatus,* must have occurred during the Pleistocene east of the Rocky Mountains and south of the Laurentide Ice Sheet. These species were probably not periglacial toads but occurred farther south.

The Dakota Toad, *B. hemiophrys,* was probably a periglacial form which occupied a range along the southern border of glaciation from Montana to Wyoming where a relict population is now found on the Laramie Plateau. This species has probably been in Montana since glaciation, but could have moved north in the xeric period between glaciation and the present, and then moved south into Montana. The Rocky Mountain Toad, *B. w. woodhousei,* could also have moved north and was then pushed south again by changing conditions and the reinvading *B. hemiophrys.*

On the slopes of the Rocky Mountains, perhaps on the bench above Glacier Wall, the bench at Granite Park, or the interlake ridge northwest of Lake McDonald, the *canorus*-like form of *B. b. boreas* was able to survive the Pleistocene glaciation. Calder and Savile (1959) have shown an analogous situation for a plant of the variety *septentrionalis* of the *Heuchera cylindrica* complex which seems to have been isolated on the eastern slopes of Glacier National Park during the last stages of Pleistocene glaciation and to have spread northward from there as the ice retreated. Karlstrom (1962) suggested that *B. canorus* in California is a montane differentiate of an ancestral *boreas*-like form which became isolated in or near its present range in the Sierra Nevada. This same possibility exists for the *canorus*-like toad at high elevations in Glacier National Park. Unglaciated refuges, several probably suitable for habitation by toads, existed at intermediate elevations in Glacier National Park. In this geographic isolation, the *canorus*-like toad could have evolved and later extended its range to where it is now found in Glacier National Park.

Climatic conditions rapidly changed after the ice withdrawal about 10,000 years ago. Temperatures rose, or rainfall decreased markedly, or both. Average yearly temperatures were probably 1-2° C higher than at present. This period has been termed the altithermal period and the hyperthermal period by Antevs (1948). With the retreat of adverse conditions in western Montana and north of the Missouri River

in eastern Montana, the bufonid members were able to reinvade the glaciated areas of Montana.

The Boreal Toad reinvaded western Montana from the nonglaciated areas around the margins of glacial Lake Missoula or from east of the Continental Divide through Beaverhead County from east-central Idaho.

The Rocky Mountain Toad and the Great Plains Toad probably reinvaded Montana from the south. Both species have moved northward within Montana. The Great Plains Toad was probably able to survive and reinvade its present range at an earlier stage by following the edge of the mountains in the montane zone which accounts for its occurrence now in Canada. *B. cognatus* has no northern competitors (unless *B. hemiophrys* which seems doubtful now), but *B. w. woodhousei* presumably competes with *B. hemiophrys* which would slow its spread even if it and *B. cognatus* survived as contemporaries.

The Dakota Toad probably moved northward from the southern border of glaciation during this xeric period and was eliminated from periglacial areas on the east flanks of the Rocky Mountains except for the relict population in Wyoming. Its present range in Montana is within those areas which were formerly covered by glaciation. This suggests that the habitat of glacial potholes and ponds created by the glaciation is very favorable for the Dakota Toad and it is able to withstand competition there from other bufonid species.

The altithermal period was followed by a cooler, more moist period termed the hypothermal by Antevs (1948). Yearly temperature averages were then about 1-2° C lower than now. This caused an increase of moisture in the low passes across the Rocky Mountains which probably permitted increase in range or crossing of the Rocky Mountains by bufonids.

The situation of *B. b. boreas* and the *canorus*-like form of *B. b. boreas* in Glacier National Park can only be postulated at present. It appears that *B. b. boreas* is reinvading the mountain slopes to approach the habitat of the *canorus*-like form at 6000 ft elevation. The *canorus*-like form probably has not migrated to any extent during the post-Pleistocene because of barriers formed by lower elevations, temperature, moisture, and habitat cover of the available migration routes. The occurrence of this toad at such high elevations where adverse weather conditions exist indicates that it is a species which is tolerant of this habitat and that it therefore has been present in this region for some time.

Summary

1. The Boreal Toad, *Bufo boreas boreas,* is found throughout intermontane Montana. It may also occur on isolated low mountain groups in the plains region.

2. A variation in the typical Boreal Toad is found at several localities at high elevations in Glacier National Park. This toad resembles *Bufo canorus* of the Sierra Nevada in California.

3. The Great Plains Toad, *Bufo cognatus*, has an extensive distribution in the short grass prairie of eastern Montana. It prefers the higher portions of the short grass prairie.

4. The Dakota Toad, *Bufo hemiophrys,* has a range within the area formerly covered with the Laurentide Ice Sheet in northern Montana east of the Rocky Mountains.

5. The Rocky Mountain Toad, *Bufo woodhousei woodhousei,* is the most wide rang-

ing of Montana toads in its distribution. Its range lies east and south of the Continental Divide.

6. A simple explanation of bufonid distribution in Montana is as follows: *B. hemiophrys* and *B. b. boreas* were periglacial toads, the former in the plains region and the latter in intermontane Montana. With warming and drying in postglacial times and especially with the approach of the altithermal, these periglacial toads withdrew northward to higher latitudes. This vacant region east of the Rocky Mountains was invaded from the south and east by *B. w. woodhousei* and *B. cognatus*. Some interspecific competition may have been involved but this can be only postulated. The *canorus*-like form of *B. b. boreas* may be a Wisconsin isolate of an ancestral *boreas*-like toad which became isolated in or near its present range in Glacier National Park and is an example of altitude convergency in very small populations.

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Literature Cited

Alden, W. C. 1932. Physiography and glacial geology of eastern Montana and adjacent areas. U.S. Geological Survey Prof. Paper 174. 133 pp.

————. 1953. Physiography and glacial geology of western Montana and adjacent areas. U.S. Geological Survey Prof. Paper 231. 200 pp.

Antevs, E. 1948. Climatic changes and pre-white man in the Great Basin, with emphasis on glacial and post-glacial times. Bull. Univ. Utah 38: 168-191.

Black, J. H. 1967. Toads of Montana. Montana Wildlife, 1967 (1): 22-28.

————. 1969. The frog genus *Rana* in Montana. Northwest Science 43: 191-195.

————. 1970a. Amphibians of Montana. Montana Wildlife, 1970 (1): 1-32.

————. 1970b. Unusual forms of the Boreal Toad, *Bufo boreas boreas* (Amphibia: Bufonidae) in Glacier National Park, Montana. Proc. Okla. Acad. Sci. 50: 127-128.

————. 1971. Breeding behavior of the Boreal Toad, *Bufo boreas boreas* (Baird and Girard), in western Montana. Great Basin Nat. In press.

————, and A. N. Bragg. 1968. New additions to the herpetofauna of Montana. Herpetologica 24: 247.

Calder, J. A. and D. B. O. Savile. 1959. Studies in the Saxifragaceae I. The *Heuchera cylindrica* complex in and adjacent to British Columbia. Brittonia 11: 49-67.

Conant, R. C. 1958. A Field Guide to Reptiles and Amphibians of the Eastern United States and Canada East of the 100th Meridian. Houghton-Mifflin Co., Boston. 366 pp.

Flint, R. F. 1957. Glacial and Pleistocene Geology. John Wiley and Sons, Inc., New York. 553 pp.

Karlstrom, E. L. 1962. The toad genus *Bufo* in the Sierra Nevada of California. Univ. Calif. Publ. Zool. 62: 1-104.

Stebbins, R. C. 1966. A Field Guide to Western Reptiles and Amphibians. Houghton-Mifflin Co., Boston. 279 pp.

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Deer Mouse Movement in Forest Habitat

Early, economical stocking of deforested areas is a major problem of foresters in the Douglas-fir (*Pseudotsuga menziesii*) belt. Many factors adversely affect regeneration efforts, such as animals, disease, weather, and others. Of the animals, deer mice (*Peromyscus maniculatus*) have received much attention because of their abundance and consumption of tree seed. The deer mouse movement in forest habitat is of importance in direct seeding operations in the Douglas-fir belt. It is recognized that *Peromyscus* soon occupy underpopulated habitat (Hooven 1963; Spencer 1955; Gashwiler 1959). Although much of this colonization is probably the result of movement from surrounding areas (Blair 1940; Stickel 1946; Hooven 1953; Gashwiler 1969b), specific data on the movement of animals in forest habitat are scantily documented. It was with the hope of adding to the understanding of this movement, and thus aiding foresters, that these data were compiled.

The investigation was made from October 1955 until October 1958 inclusive, on the H. J. Andrews Experimental Forest in Lane and Linn counties, Oregon, near the town of Blue River. The forest is located within the boundaries of the Willamette National Forest on the west slope of the Cascades. It includes the entire watershed of Lookout Creek, a tributary of Blue River.

A 48-acre clearcut (5B) and adjacent forest were selected for study. This area has an elevation ranging from about 2900 to 3500 ft and a southerly slope of about 18 percent. The terrain is bench-like alternating with steep slopes, and the soil is porous clay loam of volcanic origin (Berntsen and Rothacher, 1959). Interpolating the Berntsen-Rothacher precipitation data on the basis of elevation gives a rough estimate of about 113 inches of moisture per year.

The old-growth timber on the study area was mostly overmature and was starting to deteriorate. Percentages of sound timber logged on the clearcut were: Douglas-fir 87 percent, western hemlock (*Tsuga heterophylla*) and others 12 percent, and western redcedar (*Thuja plicata*) 1 percent. The clearcut was burned in October 1955. It was covered with ashes and charred wood when this investigation was started the latter part of the month. By the end of the study, three years after burning, total ground coverage was estimated to be about 14 percent woody plants (including coniferous reproduction) and 16 percent herbaceous species.

Methods

General study plans were to live-trap and mark deer mice on the grid in the clearcut. Soon afterward, generally the next day, lines of live-traps within the timber were also operated to live-trap, mark, and recapture the deer mice to determine the movement between the clearcut and adjacent timber (Fig. 1).

Large Sherman live-traps with wool bedding were used to capture the deer mice. They were baited mostly with scratch feed containing yellow cracked corn, wheat, and oats. The scratch was fortified with and sometimes replaced by oats during warmer periods. Traps on the grid were tended for six consecutive nights during

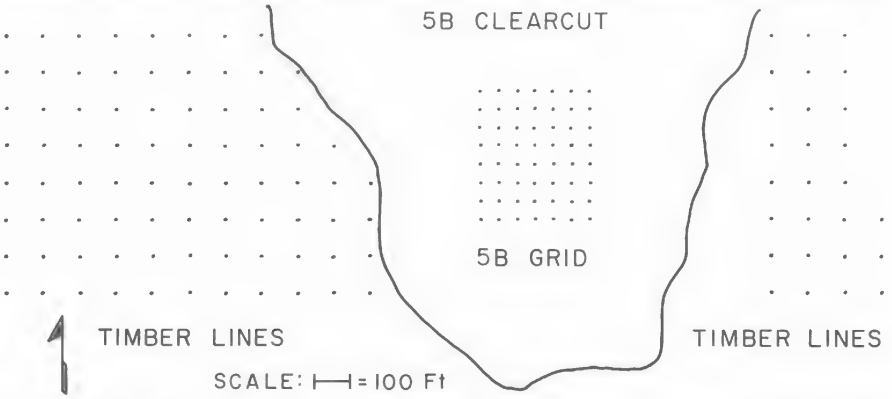

Figure 1. Map of the lower part of the clearcut showing trap sites on the grid and timber lines.

each trapping period. Ordinarily, they were run in the morning; during hot, dry periods they were kept closed during the day and opened in the evening, primarily to reduce mortality of chipmunks (*Eutamias townsendii*). Live-traps in the timber were run for three-night periods, in most cases immediately after the grid trapping. The traps were checked once a day and were left open when tended. Monel fingerling tags were used to ear-tag the animals.

The trap arrangement for the movement study is shown in Figure 1. The grid was located near the center of the east-west clearcut boundaries; trap sites were in an 8-by-7 pattern with 50-ft spacing. The trap lines used to determine deer mouse movement were placed at 100-ft intervals in adjacent timber east and west of the live-trap grid. The nearest line of traps in the timber was about 300 ft from the grid in the clearcut, and the farthest about 1700 ft.

Data were analyzed by chi-square and analysis of variance methods. The 95 percent level was selected as the criterion of significance.

In discussing results, deer mice captured and marked on the grid in the clearcut are referred to as grid deer mice, and those captured in the timber trap lines as timber deer mice.

Results and Discussion

Percentage of Recaptures

The monthly percentage of grid deer mice recaptured on the timber lines ranged from 6 to 52 and averaged 24 (Table 1). This suggests a high, relatively constant rate of interchange between the clearcut and adjacent timber trap sites when one considers that movements of less than 300 ft and over 1700 ft were not measured and that only part of the surrounding forest was sampled. The highest percentage (52) of recaptures occurred in October 1955, immediately after the clearcut was burned for cultural purposes. The fire apparently caused the deer mice temporarily to desert the clearcut for safety in the adjacent forest (Gashwiler, 1959).

TABLE 1. Number of deer mice tagged on the clearcut grid and the number and percentage recaptured on the timber lines.

Year and month	No. tagged	Tagged mice recaptured (timber)	
		Number	Percent
1955—October	21	11	52
1956—May	17	4	24
June	27	11	41
July	20	7	35
August	15	6	40
September	17	5	29
October	21	7	33
November	21	9[a]	43
Sub-total for 1955 and 1956	159	60	38
Average	20	8	--
1957—October	64	4	6
1958—May	37	4	11
October	37	3	8
Sub-total for 1957 and 1958	138	11	8
Average	46	4	----
Grand total	297	71	24
Average, all years	27	6	---

[a] Trapped two days but adjusted for three.

No definite pattern of movement in relation to months was apparent (Table 1). Movement data for 1955 and 1956 were uniformly high, averaging 38 percent, compared with 8 percent for 1957 and 1958. Plant coverage on the clearcut was sparser in 1955 and 1956 than in 1957 and 1958, suggesting a lower abundance of deer mouse plant food. This scanty food supply may have caused the mice to range more widely to meet their food requirements. This assumption agrees with Dice (1941) and Stickel (1960), who found that *Peromyscus* were more mobile under poor than good food conditions. Deer mouse population densities may have also influenced the degree of movement. The average number of deer mice tagged (Table 1) in 1955 and 1956 (20) was less than half that of 1957 and 1958 (46). This suggests that deer mouse movement is also probably greater for light than for heavy population densities. This relationship was found true for wood mice (*Peromyscus leucopus*) in Maryland (Stickel, 1960).

The possible influence of the fall of tree seed on deer mouse movement was also investigated. Although the annual seed crop was not measured on the study area, samples (seed trapping) obtained elsewhere in the Andrews Forest were probably indicative of the relative seed fall there. The number of sound (probably viable) seeds of Douglas-fir and western hemlock that fell on a clearcut in the Andrews Forest was estimated at 2400, 3500, and 14,600 per acre respectively in 1955, 1957, and 1958 (Gashwiler, 1969a), but was 158,500 per acre in 1956. This offered an opportunity to determine whether a relatively heavy seed crop attracted clearcut (grid) deer mice to the more heavily seeded forest. Isaac (1943) gave data that showed the Douglas-fir and hemlock seeds, which were from 200 to 1000 ft within the clearcut, were only one-sixth of those in the virgin forest. The seed dispersal

pattern for 1956 was as follows: The Douglas-fir and hemlock seed fall started slowly; only a trace (300 per acre) had fallen by the first third of September. By the first third of October, about 16 percent (25,800 per acre) of the total crop was shed; this increased to about 18 percent (27,700 per acre) during the first third of November.

Deer mouse recaptures for 1956 had considerable monthly variability, ranging from 24 to 43 percent with much overlapping and no marked trend toward increasing recaptures in adjacent timber as seed fall progressed (Table 1). Recaptures for the pre-seed-fall period (May to September inclusive) averaged 34 percent compared with 38 percent during seed fall (October and November) when about 28,000 sound seed per acre had fallen. These data suggest that the heavier seed fall in the timber did not attract deer mice from the clearcut to the forest habitat, at least not strongly. Since the clearcut was only lightly vegetated, and plants which produced food were probably at a low level, these results gain added credence. However, many factors were probably involved, and more information is needed to establish definitely that a heavy seed fall does not attract clearcut deer mice to the forest edge.

Sex and Age of Travelers

Questions are sometimes raised about the relative amount of movement between sexes and between ages of deer mice. The data from the grid traps were compared with those from the timber lines. If the timber line recaptures showed the same percentage of males to females and of adults to juveniles as the original captures on the grid, and vice versa, it could be inferred that movement by sex class and by age class was essentially similar.

Although monthly variations occurred, averages for the sex and age classes were similar (Table 2). The chi-square test showed no significant difference in sex and age class composition between deer mice captured on the clearcut and those

TABLE 2. Sex and age ratios of deer mouse catches by site and by month of capture or recapture.

Year and month	Total No.		Sex (% male)		Age (% adult)	
	Grid	Timber lines	Grid	Timber lines	Grid	Timber lines
1955						
October	21	11	48	27	90	100
1956						
May	17	4	59	50	100	100
June	27	11	41	55	100	100
July	20	7	45	29	85	86
August	15	6	47	50	100	100
September	17	6	35	50	82	100
October	21	7	62	71	76	86
November	21	9	52	56	71	89
1957						
October	64	13	56	77	100	100
1958						
May	37	4	54	100	34	75
October	37	8	43	25	34	100
1959						
May	4	0	50	0	4	0
Total and average	301	86	50	52	92	95

in the timber. Factors affecting movement probably had about the same influence in the two habitats. Thus it was concluded that movement was not directly attributable to any particular sex or age class.

In a California investigation, Brant (1962) found no consistent difference in movement of *Peromyscus* between sexes; however, he had poor representation of breeding females with their smaller movement patterns. He also indicated that most dispersal was by adults. On the other hand, Howard (1949) reported that juvenile *Peromyscus* in Michigan were the most active in dispersal movements. It should be recognized that dispersal is not the same as the ordinary day-by-day movements of the animals. It is apparent that differences exist in the various accounts of the relationship of sex and age classes to movement among deer mice. Many factors probably influence movement, and some variation in patterns should be expected.

Travel Distances

The distance traveled by deer mice is of importance in reforestation of clearcuts by seeding. It should also be considered when new clearcuts are planned in the vicinity of old ones, with their relatively heavy deer mouse populations which could quickly populate a new area. In this study, some of the travel distances included movement to and from the clearcut and timber; it is assumed they could move either direction with equal facility. Seventy-seven percent of the recaptured deer mice were originally tagged on the clearcut grid, and the other 23 percent on the timber lines. During this investigation, some travel data were secured by comparing the number of deer mouse recaptures per trap at various distances, and by averaging the recapture travel distances.

Recaptures per trap. The distances traveled by deer mice from the grid to the forest were determined by comparing the number of recaptures per trap at the various distances (Fig. 2). The greatest number of mice per trap were captured in the 251- to 350-ft belt. These were the nearest traps to the grid and a heavy catch was expected there. A large number of deer mice were also caught per trap in the 351- to 450-ft belt. These data indicate that a large number of deer mice traveled at least 450 ft from the grid. However, the catch per trap dropped to a relatively low level at a distance of 451 to 1350 ft, suggesting that many deer mice from the grid did not range so far. These data suggest that most of the deer mouse travel was probably less than 450 ft from the grid. About 300 ft of this would have been in the clearcut and 150 ft in the timber. Although this probably approximates the travel distance of deer mice to and from the forest, it should be kept in mind that because of trap placement, low and high movements are not represented. In addition, many mice moving from the grid probably moved beyond the effective range of the line traps, especially at the longer distances, and thereby reduced the number of recaptures.

Average distances. The individual monthly trapping distances between the grid and timber lines were also averaged (Table 3). Examination of the table shows some monthly variation in the average travel distances of males (774 ft) and females (638 ft). These data agree with the findings of Blair (1940), Stickel and Warbach (1960), and Stickel (1968), who reported that adult males generally have greater movement (larger home ranges) than adult females. However, statistical analysis revealed no significant difference between sexes and between months. When data

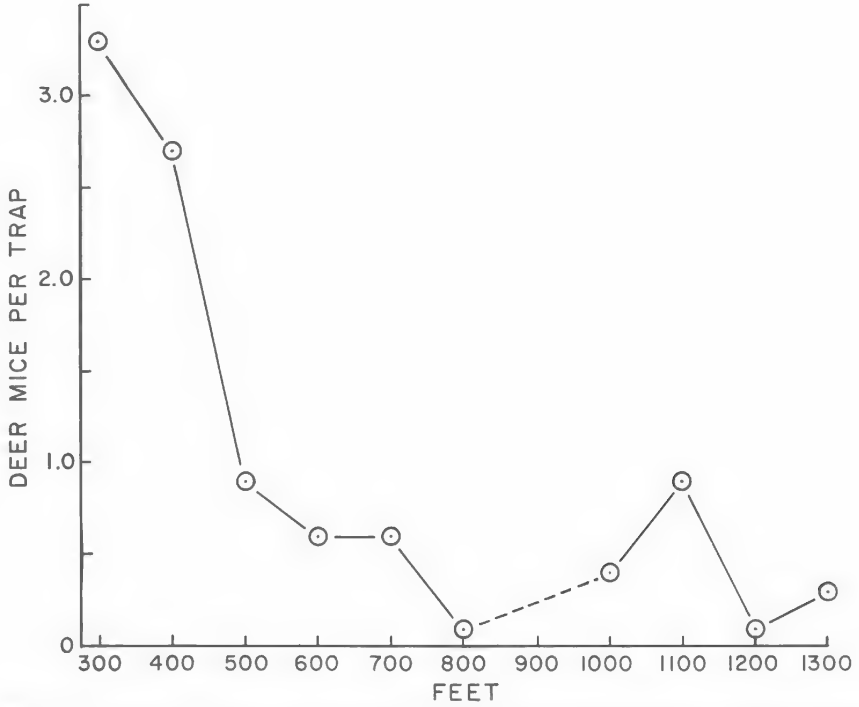

Figure 2. Number of deer mouse recaptures per trap on the timber lines at progressively greater distances from the grid in the clearcut. Distances measured at 100-ft intervals from nearest point on the grid.

TABLE 3. Average distance traveled (number of feet between the most widely separated capture sites for each animal) between the grid and timber lines by sex and by month.

Year and month	Male		Female		Total	
	No. mice	Av. distance (ft)	No. mice	Av. distance (ft)	No. mice	Av. distance (ft)
1955						
October	3	875	8	741	11	768
1956						
May	2	975	2	501	4	738
June	6	554	5	709	11	625
July	2	947	5	641	7	637
August	3	1,033	3	495	6	764
September	2	1,103	3	391	5	676
October	5	823	2	472	7	723
November	5	740	4	556	9	658
1957						
October	3	511	1	610	4	536
1958						
May	4	717	0	0	4	717
October	1	540	2	1,112	3	921
Total	36	774	35	638	71	698

on both sexes were combined, the travel distance averaged 698 ft. The maximum travel recorded was between 1400 and 1500 ft.

The data suggest that deer mice normally move about 450 to 700 ft to and from the clearcuts and adjacent timber. Since movements of less than 300 ft are not represented in the averages, it seems likely that a 700-ft belt around the perimeter of the clearcuts would include many of the deer mice that repopulate the logged areas. In efforts to alleviate the movement of deer mice into direct seeded clearcuts, this 700-ft belt would appear to merit special consideration.

Number of Trips between the Clearcut and Timber

Data were compiled to show the number of trips (originating at either point) made between the clearcut and forest by the deer mice. These data included all (126) recorded travel distances between the two areas. The number of trips and percentage of the deer mice making them are: 1—69 percent, 2—16, 3—3, 4—5, 5—2, 7—2, 8—1, 10—1, and 14—1 percent. The deer mouse who made 14 trips between the clearcut and forest is unusual and of particular interest. It was an adult male and made these trips between October 1955 and November 1956 inclusive; 13 trips were made monthly between May and November 1956. In three instances when traps were closed on the clearcut and opened the same day in the forest area, this animal made the change-over and was caught the next day at the new site. This suggests frequent, perhaps daily, movement of some of the deer mice beyond the clearcut. These data on trips are considered to be minimum figures. However, they reveal considerable movement of deer mice to and from the clearcut and timber. This movement helps to explain the high rate of population turnover of deer mice (Hooven, 1958). It also supports the conclusion of Stickel (1968) that deer mice probably have good knowledge of the terrain surrounding their home range.

Summary

In this study, 24 percent of the deer mice captured on the clearcut were also recaptured the same month in the timber. The greatest number (52 percent) was caught immediately after the clearcut was burned; no monthly recapture pattern was apparent. Food resources and population densities may have influenced the mobility of deer mice. Heavy tree seed fall did not strongly attract deer mice from the clearcut to the forest, and sex and age did not significantly influence movement, although adult males had greater average ranges than adult females. The number of animals recaptured per trap and the average travel data indicated that most of the deer mice traveled from about 450 to 700 ft between the clearcut and the timber. Forest deer mice living within this distance of clearcuts probably cause much of the repopulation problem in forest regeneration by direct seeding.

Acknowledgements

This study was made in cooperation with the Willamette National Forest and the Pacific Northwest Forest and Range Experiment Station. I would like to thank Henry J. Gratkowski for assistance in locating the study area and laying out the small mammal grid; Walter G. Dahms for helping with analysis; and Vincent H. Reid, Bureau of Sport Fisheries and Wildlife, and William H. Lawrence, Weyerhaeuser Company, for manuscript review. The help of my wife, Melva, on all phases of the work is especially appreciated.

Literature Cited

Berntsen, C. M., and J. S. Rothacher. 1959. A guide to the H. J. Andrews Experimental Forest, Pacific Northwest Forest and Range Exp. Sta. 21 p.

Blair, W. F. 1940. A study of prairie deer-mouse populations in southern Michigan. Amer. Mid. Nat. 24: 273-305.

Brant, D. H. 1962. Measures of the movements and population densities of small rodents. Univ. Calif. Publ. Zool. 62: 105-184.

Dice, L. R. 1941. Methods for estimating populations of mammals. J. Wildl. Mgmt. 5: 398-407.

Gashwiler, J. S. 1959. Small mammal study in west-central Oregon. J. Mammal. 40: 128-139.

———. 1969a. Seed fall of three conifers in west-central Oregon. Forest Sci. 15: 290-295.

———. 1969b. Deer mouse repopulation of a poisoned Douglas-fir clearcut. J. Forest. 67: 494-497.

Hooven, E. F. 1953. Some experiments in baiting forest lands for the control of small seed eating mammals. Oregon State Board Forestry, Res. Bull. 8. 70 p.

———. 1958. Deer mouse and reforestation in the Tillamook burn. Oregon State Board Forestry, Res. Note 37. 31 p.

Howard, W. E. 1949. Dispersal, amount of inbreeding, and longevity in a local population of prairie deer-mice on the George Reserve, Southern Michigan. Univ. Michigan, Contrib. Lab. Vert. Biol., No. 43. 50 p.

Isaac, L. A. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Pack Forestry Foundation, Washington, D.C. 107 p.

Spencer, D. A. 1955. The effects of rodents on reforestation. Proc. Soc. Amer. Forest. 1955: 125-128.

Stickel, L. F. 1946. The source of animals moving into a depopulated area. J. Mammal. 27: 301-307.

———. 1960. *Peromyscus* ranges at high and low population densities. J. Mammal. 41: 433-441.

———. 1968. Home range and travels, p. 373-411. *In* J. A. King (ed.), Biology of *Peromyscus* (Rodentia). Amer. Soc. Mammal. Spec. Publ. 2.

———, and O. Warbach. 1960. Small-mammal populations of a Maryland Woodlot, 1949-1954. Ecology 41: 269-286.

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Optical Dendrometer Measurement of Increment Characteristics on the Boles of Douglas-Fir in Thinned and Unthinned Stands[1]

Introduction

One economic consideration for thinning young Douglas-fir is the "redistribution of growth potential of the stand to optimum advantage, involving tree size and quality considerations" (Worthington and Staebler, 1961). Acceleration of growth in diameter and changes in tree form may be attributed to the method and intensity of the silvicultural practices applied within a stand. In the past, measurement of changes in growth and form of trees has been accomplished either by climbing or felling them. But climbing a tree to measure upper stem diameters is costly and dangerous, and a felled and sectioned tree is excluded from remeasurement.

The Forest Research Laboratory at Oregon State University has used the Barr and Stroud optical dendrometer since 1966 to provide accurate measurements of diameter and height on more than 500 standing trees for construction of volume tables under various cutting practices on experimental forests. Computers convert field data into information on growth, form, and volume.

Permanent reference points established on the ground during the initial measurement permit remeasurements of diameters at the same points at intervals. Recently, remeasurement of selected trees after a two-year growth interval indicated the practicality and advantages of periodic studies of growth by this method.

Procedure

The Barr and Stroud optical dendrometer is a sturdy precision instrument that is satisfactory and convenient in most weather and terrain (Fig. 1). It is capable of accurate measurements of trees in young Douglas-fir stands 20 years and older. The specifications, advantages, and limitations of the dendrometer have been described by Grosenbaugh (1963), Mesavage (1964), and Hartman (1966). Most consideration has been given to the use of the instrument for tree measurement in conjunction with 3-P sampling (prediction proportionate to probability; Grosenbaugh, 1963); no suggestions have been advanced for its applicability to research.

The manufacturer (Barr and Stroud, undated) claims an "uncertainty of observation" for "a good observer under average practical conditions" of 0.1 in for diameters between 1.5 and 10.0 in and 1 percent on diameters between 10 and 200 in. Accuracy of height measurements is 1.5 percent at vertical angles greater than 10 degrees. A

[1] Paper 759, Forest Research Laboratory, School of Forestry, Oregon State University, Corvallis, Oregon 97331.

study here (Bell and Groman, 1971) compared actual diameter and heights with those measured by the dendrometer under normal sighting conditions in a typical Douglas-fir stand. The data confirmed that most diameter and height values fall within the allowances claimed by the manufacturer.

Figure 1. The Barr and Stroud optical dendrometer in operation.

In our measurement program (Groman, 1970), diameter is determined at several points along the bole of each tree. The stump diameter, 4 ft dbh (6 in below stump), is estimated from a linear regression with dbh as the independent variable. The dbh on the line of sight from the dendrometer to the tree is determined by calipers to maintain the same line of sight as for measurements of the diameter with the dendrometer. Points where the caliper arms touch the tree are marked with paint dots. A vertical stripe facing the permanent reference point is also painted on the tree for identification. The permanent reference point is a railroad spike driven into the ground directly under the center of the tripod. This point is established by bearing and distance to the tree measured and to the tree nearest the point.

A 25-ft collapsible leveling rod is an integral part of the program. It eliminates sighting at the base of the tree and establishes the point for the required observation at 16.5 ft. The 4.5 ft mark on the rod is placed at dbh with the rod against the tree and facing the instrument. Several measurements are taken with the instrument along the bole; at crown base and, as required, below and above crown base. Total height of the tree is measured with a Suunto clinometer attached to the dendrometer (Groman, 1970).

For remeasurement of the tree, the dendrometer is set up over the permanent reference point. The sine value of the original 16.5 ft recording is set on the inclinometer head and the level bubble centered. The tripod tube is then raised or lowered until the horizontal line viewed through the eyepiece bisects the 16.5 ft mark on the leveling rod. The instrument is then at the same height as during the original readings.

The readings to determine height up the stem are then set off on the dendrometer and the readings for diameter made. Remeasurement time for a tree is about 20 min.

Measurements are recorded in the field on a data input card. Data are arranged

Figure 2. An unthinned stand with 285 trees per acre on the George T. Gerlinger Experimental Forest at Black Rock. Basal area is 256 sq ft. Average dbh is 12.8 in.

and coded so that the completed cards can be taken directly to the computer center to be key-punched. Field data are converted with a modification of Grosenbaugh's (1963) exact theory computer program. Information is also available for a variety of volumetric information.

With this procedure, 200 trees in a site III stand of 55-year-old Douglas-fir were measured in 1967 on the Black Rock unit of the George T. Gerlinger State Experimental Forest. Trees observed were in unthinned areas (Fig. 2), areas lightly and frequently thinned, a heavily thinned area, and a very heavily thinned area (Fig. 3).

Results and Discussion

After two growing seasons, several of the trees in each of the thinning classifications were remeasured at the same points on the stem to test the method. Differences in growth patterns among trees of the same dbh, height, and crown class were apparent in this sampling. For example, the greatest difference in diameter growth between

Figure 3. A stand thinned to 52 trees per acre. George T. Gerlinger Experimental Forest at Black Rock. Basal area is 124 sq ft. Average dbh is 21.0 in.

trees of similar size occurred in the unthinned and the very heavily thinned plots (Figs. 4, 5, 6). Trees from plots thinned lightly and frequently generally showed an intermediate position between unthinned and heavily thinned plots.

Dominant and codominant trees in thinned stands showed accelerated growth in diameter and a more consistent increment along the entire bole. Dominant and codominant trees in unthinned stands, however, had their greatest increment on the upper portion of the bole.

Intermediate trees followed the same pattern, except that growth in diameter of trees in unthinned stands or trees in direct competition with larger trees in thinned stands appears to be even more concentrated in the crowns.

The remeasurements demonstrated that use of the optical dendrometer along with permanent reference points and a computer program will enable investigators to study the complex relations that determine the development of individual trees and stands without destructive sampling.

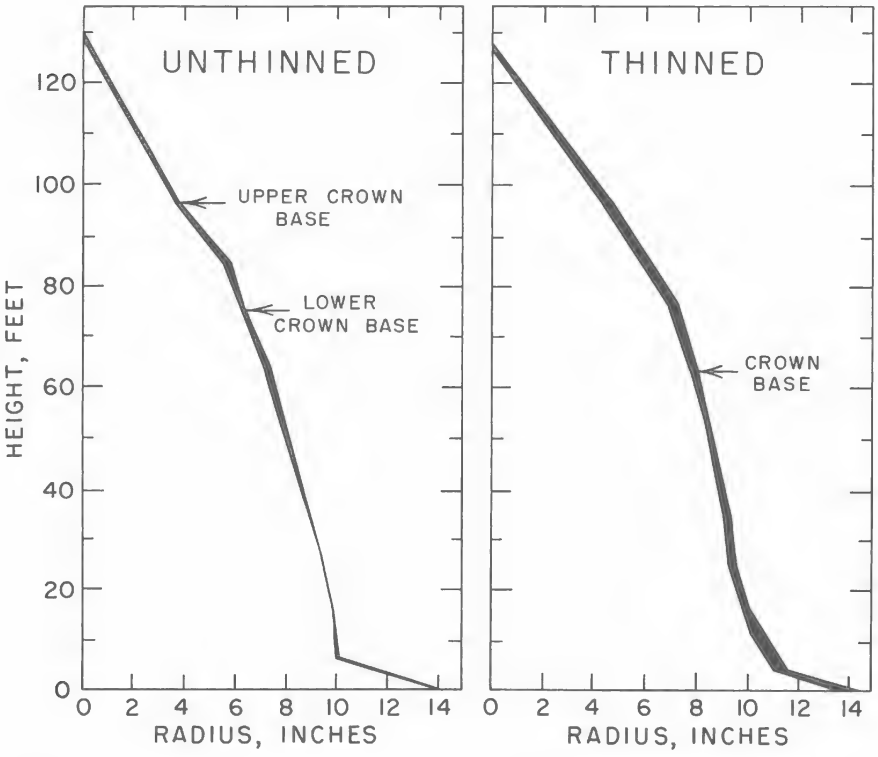

Figure 4. Two-year growth (1967-69) in radius outside bark of two dominant trees, both 22.1 in dbh and of similar height in 1967. The accelerated growth as well as the uniformity of increment along the stem of the tree in the thinned stand is apparent. Growth on the tree in the unthinned stand is less uniform and does not show any discernible increase in the lower stem. Cubic foot volume of the tree in the unthinned stand increased 3.9 percent and, in the thinned stand, 9.4 percent. Arrows indicate crown base.

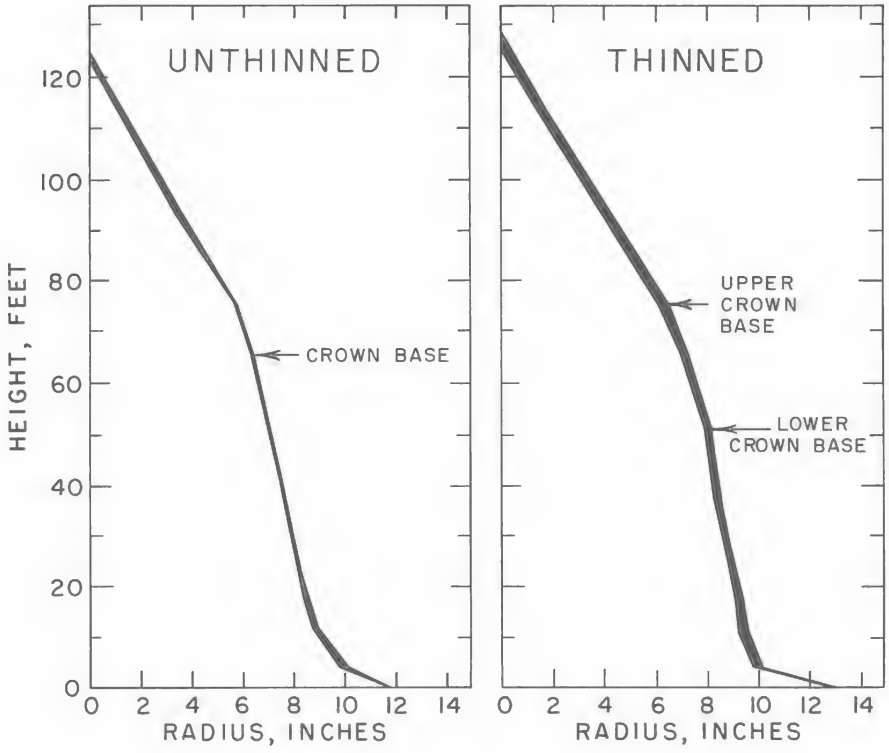

Figure 5. Two-year growth (1967-69) in radius outside bark of two dominant trees with 1967 dbh of 19.6 in. Again the accelerated growth, as well as the more uniform growth along the bole, of the tree from the thinned stand is evident. The tree in the unthinned stand placed more new wood on the lower portion of the stem than the unthinned tree in Figure 4. Cubic foot volume of the tree in the unthinned stand increased 5.1 percent; tree in the thinned stand, 9.2 percent. Arrows indicate crown base.

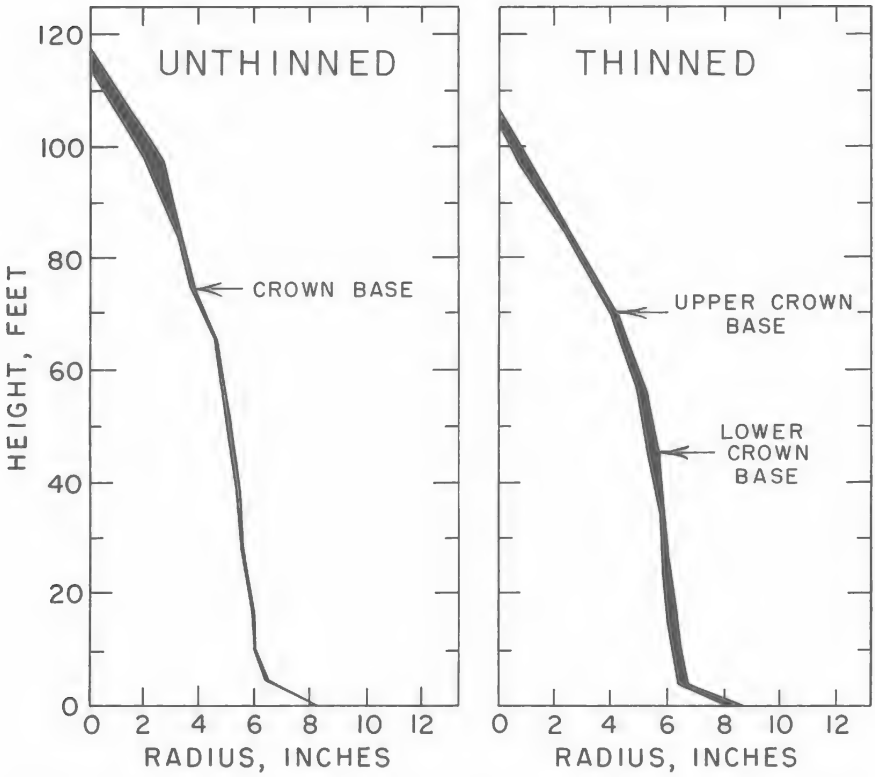

Figure 6. Two-year growth (1967-69) in radius outside bark of two codominant trees, both 12.8 in dbh in 1967. The tree in the unthinned stand is about 10 ft taller than the tree in the thinned stand. The uniform diameter growth is still apparent on the tree in the thinned stand. A different distribution of increment is evident on the tree in the unthinned stand with a large increase in radial growth on the bole within the crown. Cubic foot volume of the tree in the unthinned stand increased 7.4 percent; tree in the thinned stand, 13.6 percent. Arrows indicate crown base.

Literature Cited

Barr and Stroud. Undated. Instructions for the use and care of the Barr and Stroud dendrometer type FP12. Barr and Stroud Limited, Glasgow, Scotland. Pamphlet 1468.

Bell, J. F., and W. A. Groman. 1971. A field test of the accuracy of the Barr and Stroud optical dendrometer. Forestry Chron. 47(2) 1-6.

Groman, W. A. 1970. Application of an optical dendrometer program for young-growth Douglas-fir management. *In* A. B. Berg [ed.] Proceedings, Management of Young Growth Douglas-fir and Western Hemlock. Oregon State University, Corvallis.

Grosenbaugh, L. R. 1963. Optical dendrometers for out-of-reach diameters: a conspectus and some new theory. For. Sci. Monograph 4.

Hartman, G. B. 1966. Some practical experience with 3-P sampling and the Barr and Stroud dendrometer in timber sales. Proceedings, Soc. Amer. Foresters. Pp. 126-130.

Mesavage, C. 1964. Aids for using Barr and Stroud dendrometers. Proceedings, Soc. Amer. Foresters. Pp. 238-244.

Worthington, N. P., and G. R. Staebler. 1961. Commercial thinning of Douglas-fir in the Pacific Northwest. U.S. Dept. of Agric., Tech. Bull. 1230.

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Mortality of Adult Eulachon (Thaleichthys pacificus) Subjected to Sudden Increases in Water Temperature

Increased industrial use of water and the construction of nuclear plants, storage reservoirs, and dams are expected to change the thermal regime of the Columbia River. Moore (1968) and Clark and Snyder (1970) reported that temperatures in the lower river have already increased.

Fry (1947) pointed out that temperature affects animal activity through metabolism. Temperature governs the amount of energy available for such activities as swimming, feeding, digesting food, and spawning. Brett (1960) stated that water temperature for any species of fish should not exceed that which would curtail activity below three-fourths of the optimum. If activity is depressed, survival of the species is in jeopardy. The energy demands for reproduction impose thermal limitations if the species is to survive. Brett recommends a "freedom" of 3 C (5.5 F) below the ultimate lethal level.

The Columbia River has commercially important runs of eulachon (*Thaleichthys pacificus*) each year (Pruter, 1966). Smith and Saalfeld (1955) report that in the past, large numbers have spawned in the Grays, Cowlitz, Lewis, and Sandy rivers—tributaries of the Columbia River. They add that the runs to tributaries farthest from the mouth of the Columbia are sporadic and may be absent in some years. The commercial and sport fisheries in the Cowlitz River remain the most productive.

Smith and Saalfeld (1955), in three series of tests, found that eulachon exhibited an aversion to three different waste flows from industrial sources. They also reported that the eulachon showed a preference for a narrow range of water temperature; the fish entered the Columbia River and its tributaries when the river temperature was between 2 and 10 C.

Water temperatures above this range could result from the operation of a thermal nuclear power plant. For example, increases in water temperature near the outfall of a 2000 MWe plant can be expected to reach a ΔT[1] of 11.1 C at the plume head (Battelle-Northwest, 1967) and cause an overall increase in the entire receiving body of water after mixing. Flow reversals in the Columbia River, at the confluence of the Cowlitz, could compound the heating effect caused by effluents from proposed thermal plants in this stretch of the river (Clark and Snyder, 1969). The eulachon migrate through this area to enter the Cowlitz River.

Tests were conducted in 1968 and 1969 to examine some aspects of the thermal tolerance of the adults. Samples of eulachon were subjected to lethal and sublethal temperatures. Their resistance times and survival were recorded.

[1] ΔT = increase above ambient water temperature.

Fish Capture and Pretest Holding

Eulachon (Fig. 1) were dipnetted from the Cowlitz River during March 1968 and February 1969 and transported in a tank truck to the experimental temperature laboratory at Prescott, Oregon. Each trip took less than two hours, during which time oxygen was metered into the water. The average weights and fork lengths of the fish captured in 1968 and 1969 were 153 mm and 26 g, 161 mm and 31 g, respectively. The fish were sexually mature but none had spawned. They were assumed to be acclimated to the water temperature of the Cowlitz River, which was 10 C in 1968 and 5 C in 1969.

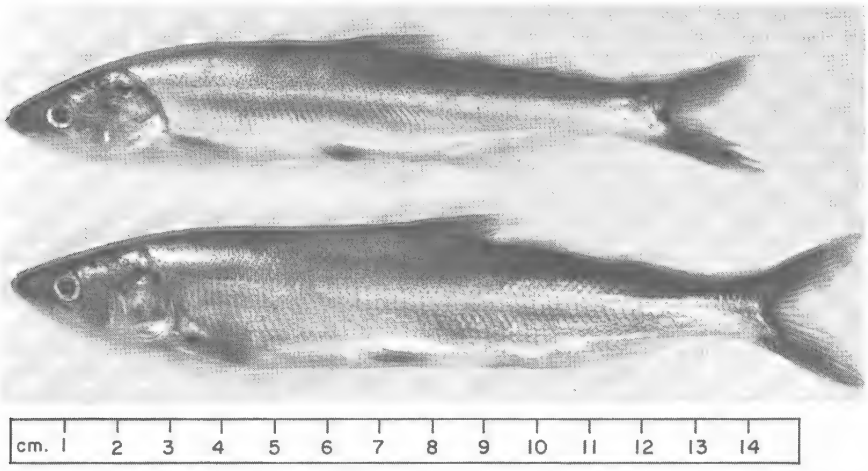

Figure 1. Adult female (above) and male eulachon (*Thaleichthys pacificus*). The scale is in centimeters.

The fish were held in 1.8 x 1.2 m redwood tanks for two days before testing to determine mortality from the stress of handling and transporting. No mortality was recorded during transport and less than 0.1 percent after the two-day holding period. Water from the Columbia River was circulated through the tanks at about seven liters per minute, which gave at least one complete interchange of water each hour. The temperature was maintained within 0.5 C of the temperature of the Cowlitz River at time of capture.

Physical Equipment and Operating Procedure

The wooden test tanks, 80 x 60 cm, were filled to a capacity of 188 liters. Water was replaced in each tank at a rate of 3.8 liters per minute, which provided at least one complete interchange of water each hour. Two air stones, plus the high rate of water exchange, maintained dissolved oxygen at 100 percent saturation or higher.

Water was supplied to the test tanks by gravity flow from two reservoirs, each with a capacity of over 3000 liters. The water in one reservoir was heated to 33 $\pm$ 0.5 C by a 100-kw heater that was thermistor controlled. The water in the second was cooled to 5 $\pm$ 0.5 C by a water chiller with a capacity of 544 kilocalories/min. Water from the two reservoirs was mixed to produce the temperature range (5-32 C) required in the test tanks. The water temperature in each tank was held within $\pm$ 0.5 C of the test temperature and monitored by a thermistor thermometer.

Testing Procedure and Results

Procedures for lethal temperature determinations for fish have been outlined and recommended by various experimenters. We chose the procedures recommended by Fry (1947) and used by Brett (1952).

1968 Tests

The 1968 tests were exploratory; however, the results were used in developing the design for the 1969 test series.

Samples of 10 fish each were immersed for one hour in one of eight test tanks that had been preheated to temperatures of 10 (control), 13, 15, 18, 21, 24, 27, or 32 C (Table 1). At the end of one hour the temperatures were lowered to 10 C within

TABLE 1. Mortality of adult eulachon subjected to various water temperatures for one hour; tested in 1968.[1]

Test water temperature	Temperature increase	TIME TO: First mortality	50% mortality	100% mortality
C		Minutes		
10	None	------	------	------
13	+3	------	------	------
15	+5	------	------	------
18	+8	36.0	1920.0	------
21	+11	15.0	26.0	------
24	+14	5.0	14.0	51.0
27	+17	1.4	2.0	3.3
32	+22	0.3	0.3	0.3

[1] One sample of ten fish was used in each test; live fish were held for 50 hours after each test.

about ten minutes. The fish were held for 50 hours after each test. The time was recorded to first mortality, 50 percent mortality, and 100 percent mortality (Table 1).

A one-hour exposure to the sudden temperature increase was chosen to represent roughly the conditions which the animals might possibly experience in a "thermal plume" during a river flow reversal.

Fish exposed to an increase of 3 or 5 C above the control (acclimation) temperature of 10 C did not die within the one-hour exposure nor during the 50-hour post-test holding period (Table 1). At least 50 percent of the test fish died, however, after exposure to a sudden increase of 8 C or more above the control temperature.

The time to first mortality, 50 percent mortality, and 100 percent mortality of fish in a sample decreased with increasing temperatures: at 18 C, 50 percent mortality was recorded in 1920 minutes; at 32 C, all fish in the sample died within 0.3 minute. A lethal level was established at 18 C; this level, however, can be altered by a change in the base acclimation temperature and exposure time.

1969 Tests

The water temperature in the Cowlitz River was lower by 5 C in 1969 than in the previous year. At the time the test fish were captured the river temperature was 5 C. The 1969 tests differed from the 1968 tests in that the range from base to highest temperature was narrowed (5 to 29 C). The animals were held at the test temperatures until death or until termination of test at 11,520 minutes (eight days). Sample

size was increased to 20 fish. Time to mortality was recorded for the fish in each sample. All other procedures were essentially the same as for the previous tests.

The incipient lethal level[2] was established at 11 C, which was 6 C above the control (acclimation) temperature (Table 2). Mortality of 100 percent was recorded at 11 C and above. Resistance times decreased with increasing temperature.

TABLE 2. Mortality of adult eulachon subjected to increased water temperatures for an eight-day test period; tested in 1969.[1]

Test water temperature	Temperature increase	TIME TO: First mortality	50% mortality	100% mortality
C		Minutes		
5	None	7380	------	------
8	+3	8880	------	------
11	+6	6360	8940	11,520
14	+9	4320	8640	10,080
17	+12	361	4860	8640
20	+15	71	4440	6120
23	+18	2	5.1	59
26	+21	0.8	1.2	1.5
29	+24	.2	.7	1.0

[1] One sample of 20 fish was used in each test.

Effects of Increased Temperature

The most profound difference between the two years of tests is that in 1968 the fish were subjected to a 60-minute exposure to the test temperatures, whereas in 1969 the fish were held at the test temperatures until death or until the eight-day test period had elapsed. The eight-day test period was chosen to provide an approximate duration of 10,000 minutes, used as a criterion by other experimenters.

The base (acclimation) temperatures in the two years of tests differ by 5 C. The difference in exposure time to test temperatures will not allow us to make resistance time comparisons between the two tests. The results of the 1968 test seem to indicate that a 60-minute exposure to a temperature of 18 C or to a +8 C thermal plume differential would cause an unacceptable mortality level.

In the 1969 tests, we were able to establish an upper incipient lethal level for eulachon acclimated to 5 C (Table 2). An exposure to a temperature increase of +6 C above 5 C ambient for 8940 minutes resulted in a 50 percent mortality. As the test temperature increased, the temperature "dose" causing 50 percent mortality was reached in less time (Table 2).

At the higher temperatures, 23 through 29 C, the fish exhibited a stress-panic reaction and their swimming movements were not directional. At 26 and 29 C, 100 percent mortality occurred in 1.5 minutes or less; it is doubtful if any of these fish could have escaped from a thermal plume by their own volition.

It was noted that the temperature-treated females had retained their eggs at death or at the conclusion of the tests; however, the control group had deposited sperm and eggs in the control tank. Approximately 1000 fish (not used in tests)

[2] The temperature beyond which 50 percent of the population can no longer live for an indefinite period of time.

had been held at river temperature during the test period in 1969. These animals spawned in the tank; fertilized and developing eggs were found as were newly hatched larvae. This indicates that the increased temperature had affected the spawning cycle of the test fish.

The data reported here are not conclusive; the lethal levels and resistance times could be altered by changing environmental conditions and the state of maturation of the animals at the time of testing. However, our data do indicate a need for exploration to assess the effects of sublethal temperature exposure on the animals' ability to spawn successfully and carry out functions necessary to survive in a changing environment.

Literature Cited

Battelle-Northwest. 1967. Summary report on nuclear power plant siting in the Pacific Northwest for the Bonneville Power Administration, Contract No. 14-03-67868. Battelle Mem. Inst., Pac. Northwest Laboratories, Richland, Washington, 50 pp. (Processed)

Brett, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Bd. Can. 9: 263-323.

————. 1960. Thermal requirements of fish—three decades of study, 1940-1970. *IN:* C. M. Tarzwell (compiler), Biological problems in water pollution, pp. 110-117. U.S. Dept. Health, Educ., Welf., Public Health Serv., Robert A. Taft Sanit. Eng. Center, Cincinnati, Ohio, Tech. Rep. W60-3.

Clark, S. M., and G. R. Snyder. 1969. Timing and extent of a flow reversal in the lower Columbia River. Limnol. Oceanogr. 14: 960-965.

————and————. 1970. Limnological study of lower Columbia River, 1967-68. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 610. 14 pp.

Fry, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud., Biol. Ser. 55, Ontario Fish Res. Lab. Publ. 68. 62 pp.

Moore, A. M. 1968. Water temperatures in the Columbia River Basin, July 1966 to September 1967. U.S. Dep. Int., Geol. Survey, Open-file report, Portland, Oregon.

Pruter, A. T. 1966. Commercial fisheries of the Columbia River and adjacent ocean waters. U.S. Fish Wildl. Serv., Fish. Ind. Res. 3(3): 17-68.

Smith, W. E., and R. W. Saalfeld. 1955. Studies on the Columbia River smelt (*Thaleichthys pacificus*). Wash. Dep. Fish., Fish. Res. Pap. 1(3): 3-26.

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The Periodicity of Spore Release from a Conifer, a Liverwort, and a Bracket Fungus

Field observations of pollen and spore release from plants are relatively rare. This study represents a continuing attempt to gather this basic information from a variety of native plants in the Pacific Northwest. The Kramer-Collins samplers were set up primarily to observe pollen release from *Tsuga* at the actual source, but interesting data were also obtained from nearby sporulation of *Ganoderma* and the liverwort *Cephalozia.* The samplers were set up for a 10-day period, but the seven days presented in this paper represent the peak period of pollen release from *Tsuga.* Data are also mentioned from a similar experiment at a lower elevation. An attempt was made to correlate the hourly fluctuations in spore release with temperature, relative humidity, cloud conditions, and precipitation.

Study Sites

This study was done between May 8 and 18, 1968, at the junction of Coal Creek and Glacier Creek (elevation ca. 3500 ft), Mt. Baker National Forest, Whatcom County, Washington. The primary canopy vegetation types in the area were *Tsuga heterophylla* (Raf.) Sarg., *Pseudotsuga menziesii* (Mirb.) Franco, *Alnus rubra* Bong, and *Salix scouleriana* Barr. At slightly higher elevations *Abies amabilis* (Dougl.) Forbes and *Alnus sinuata* (Regel) Rydb. were also present. *Cephalozia media* Lindb. was quite common on mossy logs in the vicinity. Basidiocarps of *Ganoderma applanatum* (Pers. *ex* Wallr.) Pat. were distributed from ground level to 20-30 ft high on standing dead *Tsuga.* At least 25 basidiocarps were noted within a 50-ft radius of the sampling apparatus.

Additional experiments were carried out in the Lake Louise region of Whatcom County (elevation ca. 500 ft). Sampling at this site was done on *Alnus rubra* and *Thuja plicata* D. Don.

Methods

Sampling was done with two Kramer-Collins samplers operated by 12-volt D.C. storage batteries (Kramer and Pady, 1966). The samplers operate volumetrically, sampling approximately 10 cu ft (228 liters) of air each hour taken in four equal samples. Each sample is superimposed on a single hourly band. The bands are located on a silicone grease-coated glass slide which ultimately results in a slide with 24 bands, one for each hour per day. The slides were changed at approximately 0700 hours PDT each day. Each sampler was placed under a pollen-shedding *Tsuga heterophylla* tree at ground level in sampler 1 and 1 meter higher in sampler 2. Sampler 1 was directly under a pollinating tree and at sampler 2 the male strobili were placed directly adjacent to the sampler inlet. A representative spore sample of the hourly band was counted, and a correction factor applied to express the data

in spores/cu ft/hour. Temperature and relative humidity were taken with a Bendix hygrothermograph located in a protective box at the sampling site. Notations on precipitation and cloud cover were taken at the Glacier ranger station located 3.5 air miles from the sampling site. No data were available for wind speed and direction at the sampling site.

The pollen and spores collected in the air were compared with materials collected in the vicinity for positive identification. Voucher specimens for the plants studied are deposited in the herbarium at Western Washington State College.

Results

Tsuga. At the Glacier Creek site well-defined peaks were noted on three days: May 9, 10, and 11 (Fig. 1). These peaks occurred only when the relative humidity

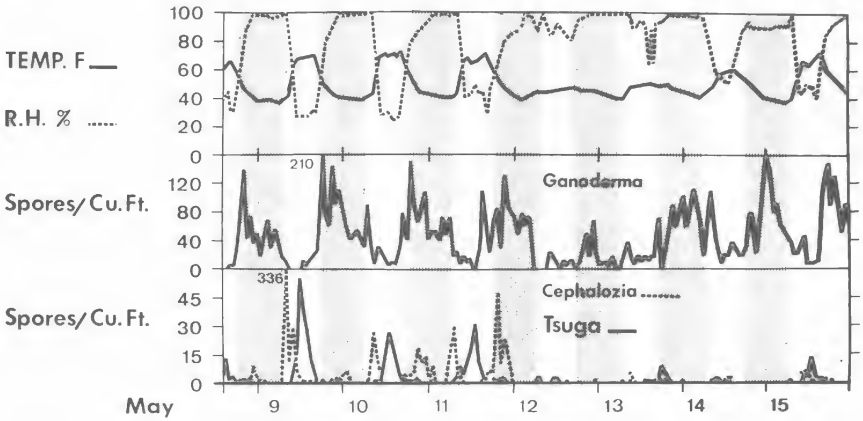

Figure 1. Hourly environmental data and volumetric spore counts from *Ganoderma, Cephalozia* and *Tsuga.*

was at the lowest point for the day. The peaks in spore numbers came at 1200 hours on May 9 and 10 and 1300 hours on May 11 when the relative humidity was at 29, 26, and 43 percent, respectively. An identical experiment carried out on *Alnus rubra* and *Thuja plicata* in the Lake Louise area of Whatcom County indicated a very similar pattern of release, but in this case the exact release time for each species was sometimes several hours apart. Visual observations of *Tsuga* strobili showed some pollen the morning of May 12, but a rainy period starting on the previous night essentially terminated pollen release for the duration of the observations.

Ebell and Schmidt (1959) studied pollen release from *Thuja plicata, Tsuga heterophylla,* and others. Using a nonvolumetric technique they found 90 percent of all pollen released during the 0800-2200 hours with the maximum release period occurring between 1000 and 1600 hours. In addition they noted the peaks were more closely related to each particular site rather than a characteristic pattern of release for each species. This variation in the daily afternoon peaks was thought to be an environmental reaction. Ogden, Hayes, and Raynor (1969) recorded pollen release from *Phleum, Zea, Ricinus,* and *Ambrosia* in cultivated plots. They showed that although the mean peak and duration of pollen release varied for each species, the pollen-shedding period was generally during the hours when relative humidity was lowest and wind speeds and/or atmospheric instability increased, except for

Phleum which began releasing pollen during the night. Similar observations on pollen release from *Humulus lupulus* L. were made by Brooks and Puri (1963) and on *Plantago lanceolata* L. by Mathews (1965).

Visual observations of the male strobili of all species studied indicated a probable hygroscopic mechanism in which the microsporangia remain closed until drying conditions prevailed. Bianchi, Schwemmin, and Wagner (1959) reported that dehiscence and extension of the anthers in *Ambrosia* were induced by changes in temperature and relative humidity that commonly occur in the field following sunrise. Ogden, Hayes, and Raynor (1969) noted that no relationship was found between temperature and pollen emission except as temperature causes changes in relative humidity.

Cephalozia. On May 8 there was a weak peak of 10 spores/cu ft at 2300 hours when the relative humidity was 100 percent. The peak that occurred on May 9 was at 0800 hours with 100 percent relative humidity just prior to a sudden drop in relative humidity and a rise in temperature. A minor peak also occurred at 0100 hours May 10 of eight spores/cu ft two hours after the relative humidity reached 100 percent. Two additional peaks occurred at 0900 hours and 2000 hours of 26 and 20 spores/cu ft, respectively. These peaks again occurred when the temperature and relative humidity were actively changing, specifically at a relative humidity of 85 and 88 percent. The data from May 12 were similar to May 11, showing peaks at 0700 hours and 1900 hours of 28 and 45 spores/cu ft. These peaks occurred at 100 and 68 percent relative humidity again when the temperature and relative humidity were undergoing active changes. The rainy period which began on May 12 coincided with a termination of any large numbers of *Cephalozia* spores in the atmosphere although a few spores were noted on May 13, 14, and 15.

Cephalozia bicuspidata, its mechanism of sporangium dehiscence, and reaction of elators to drying conditions were considered by Ingold (1965). These data showed that *Cephalozia bicuspidata* will only release its spores while the environmental conditions are actively changing. This apparent sensitivity to environmental change results in two peaks per day, one in the morning and the other in the evening when temperature and relative humidity are showing the greatest fluctuation. The evening peak is quite puzzling because in the laboratory the elators of these liverworts only show their hygroscopic activity under drying conditions.

Ganoderma. May 8 through May 11 were relatively warm days with no precipitation. The hourly maxima in spore numbers were quite similar for each of the first four days during this period. The night of May 8 showed a major peak in spore numbers of 120 spores/cu ft at 1900 hours when the relative humidity was 90 percent; another minor peak of 60 spores/cu ft occurred at 0300 hours on May 9. The spore numbers during the daytime temperature maximum and the low in relative humidity during May 9 declined to none or a trace as they did on the succeeding two days when similar conditions prevailed. The peaks on the night of May 9-10 were at 1800, 2100, and 0700 hours, and were 210, 160, and 98 spores/cu ft when the relative humidity was 80, 98, and 100 percent, respectively. As on the night of May 8-9 the early evening peak was the major one. The peaks in spore numbers for May 10-11 fell into a similar pattern with the major peak recorded at 7 P.M. and minor peaks at 2300, 0500, and 0700 hours. The afternoon of May 12 was the beginning of a rainy period and showed a 3 P.M. peak of 98 spores/cu ft when the relative humidity was 48 percent; subsequent night peaks did develop,

however, at 1900, 0200, and 0400 hours. May 12, 13, and 14 were rainy and the temperature and relative humidity were relatively constant. The spore numbers on May 12-13 showed a tendency for a night peak but were ill defined. During May 13 there was a dip in the relative humidity at 1400-1600 hours with a peak at 1700 hours of 72 spores/cu ft. The nighttime spore numbers on this night were relatively uniform, not showing the early-evening peak that seems to be prominent when the temperature and relative humidity fluctuate sharply during a 24-hour period. This pattern was re-established on May 14 through May 28 as dry weather conditions were re-established.

In studying spore release at the source, Haard (1967) and Riley (1952) found that a second early-morning peak is sometimes evident. These data showed a similar second peak on May 8 through 11, but it was ill defined. De Groot (1968), on the other hand, found a single nighttime peak in *Ganoderma* spores when sampling was carried out remote from the spore source. The data from his paper showed an intermediate situation probably because of the extremely high number of *Ganoderma* basidiocarps in the vicinity.

Discussion

The mechanism of pollen release from *Tsuga heterophylla* is apparently moisture dependent. This dry weather release pattern has been observed in many plant genera. These data show an identical pattern of pollen release in *Thuja, Tsuga,* and *Alnus.* The precise time of peak numbers in pollen grains varies from genus to genus and also from site to site (Ebell and Schmidt, 1959). Field observations of pollen strobili of these genera have supported previous observations (Bianchi, Schwemmin, and Wagner, 1959) that the microsporangium wall is hygroscopic and actually ejects the pollen as the walls contort under drying conditions.

Ingold (1959, 1965) and others have studied the mechanisms of spore discharge in the bryophytes, but these data are the first observations of spore release from a liverwort under field conditions. Since *Cephalozia* shows two peaks per day rather than one as the author expected, more field observations of this liverwort and other bryophytes are in order.

Spore release and dispersal from the species of *Fomes* and *Ganoderma* have been studied by Haard (1967), De Groot (1968), and Riley (1952). These observations tend to support previous data on spore release and dispersal from these fungi. It is interesting to compare the single nighttime peak as recorded by De Groot (1968) and the double peak recorded by Haard (1967) and Riley (1952). In the author's opinion this is an intermediate situation between the two, the former being a measurement of atmospheric dispersal and the latter the pattern of spore release at the source.

Summary

Two Kramer-Collins air samplers were placed in close proximity to *Tsuga heterophylla, Cephalozia media,* and *Ganoderma applanatum* for seven days. Hourly sampling showed three distinctly different diurnal patterns in spore release. Under normal dry weather conditions, *Ganoderma* produced broad night peaks. *Tsuga* released pollen during the early afternoon hours when the relative humidity was at the lowest point. *Cephalozia* produced as many as two peaks per day, one in the early morning and the other in the early evening approximately 12 hours apart. Under intermittent rainy conditions, *Ganoderma* spores were detected in a weak diurnal pattern; *Cephalozia* and *Tsuga* were barely detectable.

Literature Cited

Bianchi, D. E., D. J. Schwemmin, and W. H. Wagner, Jr. 1959. Pollen release in the common ragweed (*Ambrosia artemisii folia*). Bot. Gaz. 120: 235-243.

Brooks, S. N., and Y. P. Puri. 1963. Atmospheric conditions influencing pollen shedding of hops (*Humulus lupulus* L.). Crop Sci. 3: 530-531.

De Groot, R. C. 1968. Diurnal cycles of airborne spores produced by forest fungi. Phytopathology 58: 1223-1229.

Ebell, L. R., and R. L. Schmidt. 1959. Effect of elevation and climatic factors on production and dispersal of coniferous tree pollen. Proc. Soc. Amer. Foresters 39: 1-27.

Gregory, P. H. 1961. The microbiology of the atmosphere. Leonard Hill, London.

Haard, R. T. 1967. The periodicity of spore release in the hymenomycetes. Ph.D. thesis, Kansas State University. 104 pp.

Ingold, C. T. 1959. Peristome teeth and spore discharge in mosses. Trans. Bot. Soc. Edinburgh 38: 76-88.

Ingold, C. T. 1965. Spore liberation. Clarendon Press, Oxford.

Kramer, C. L., and S. M. Pady. 1966. A new 24-hour spore sampler. Phytopathology 56: 517-520.

Mathews, J. N. 1965. Dinural variation in the release of pollen by *Plantago lanceolata* L. Proc. Limn. Soc. of New S. Wales 90: 231-237.

Ogden, E. C., J. V. Hayes, and G. S. Raynor. 1969. Diurnal patterns of pollen emission in *Ambrosia, Phleum, Zea* and *Ricinus*. Amer. J. Bot. 56: 16-21.

Riley, C. G. 1952. Studies in forest pathology IX. *Fomes igniarius* decay of poplar. Can. J. Bot. 30: 710-734.

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Factors Affecting Endrin Content of Endrin-Coated[1] Douglas-Fir Seed

During the past 15 years, endrin (1,2,3,4,10,10-hexachloro-6,7-epoxy-1,4,4a,5,6,7,8,8a-octahydro-1,4-endo-endo-5,8-dimethanonaphthalene) has been extensively used to protect direct-sown forest tree seeds from seed-eating rodents (Mann, 1968; Radwan, 1970). In the Pacific Northwest, although early field tests showed that adequate stocking with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) was possible when endrin-coated seed was used (Dimock, 1957; Dick *et al.,* 1958; Roy, 1961), many operational seedings have failed. Preliminary bioassays and chemical analyses of treated seed in our laboratory indicated that some seeding failures could be due to insufficient endrin on the seed. We subsequently investigated effects of treatment, sowing by helicopter, and weathering in the field after seeding on the endrin content of treated Douglas-fir seed.

Materials and Methods

Endrin treatments. Six lots of endrin-treated seed were obtained from the 1968-69 inventories of four forest-management organizations in Oregon and Washington. All seeds were treated with Endrin 50-WP[2] (50 percent wettable powder) from Stauffer Chemical Company, using the adhesive Dow Latex 512-R (diluted 1 adhesive:9 water) from the Dow Chemical Company. Other pertinent information for each lot is shown in Table 1.

Sowing by helicopter. In February 1969, seeds from lots 5 and 6 were sown in the field by helicopter at approximately ¾ pound per acre. After sowing, seed samples of each lot were picked up from the ground and sent to the laboratory for analysis. Additional seed for analysis was obtained by simulated sowing of seed from lots 3 and 4. In each case, 1-pound samples were run through mechanical seeders of two different grounded helicopters with equipment set to deliver the same amounts of seed as those used to sow seed of lots 5 and 6. Samples of "sown" seed were collected on plastic sheets laid under the helicopters.

Weathering. In May 1969, seeds were collected for analysis from areas which were sown in February 1969 with seeds of lots 5 and 6. Only 500 seeds of each lot were collected since seed was difficult to find after exposure of about three months in the

[1] This article reports research involving pesticides. It does not contain recommendations for their use nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate state and/or federal agencies before they can be recommended.
[2] Mention of chemical products and chemical companies does not represent endorsement by the U.S. Department of Agriculture.

field. Attempts to collect "weathered" seeds from the area seeded with lot 3 were unsuccessful.

TABLE 1. Seed identification and endrin-treatment data as supplied by study participants.

Seed lot[a]	Organization	Active endrin	Chemical used for identification	Party treating the seed
		Percent by weight		
1	A	0.5	Aluminum powder	Organization A
2	B	.6	Monastral green	Commercial contractor No. 1
3	B	.6	Monastral green	Commercial contractor No. 1
4	C	1.0	Aluminum powder	Organization C
5	D	1.0	Aluminum powder	Commercial contractor No. 2
6	D	.5	Aluminum powder	Commercial contractor No. 2

[a] Seeds of lots 1 and 4 were wet with a slurry of endrin in the adhesive and then topped with the aluminum powder. Seeds of lots 2 and 3 were wet with a slurry of endrin and Monastral green (from the DuPont Co.) in the adhesive. Seeds of lots 5 and 6 were wet with a slurry of endrin and a small amount of aluminum powder in the adhesive and then topped with more aluminum powder; weight of endrin added was approximated by volume in a previously calibrated container.

Determination of endrin content. Samples of 200 seeds each were used for each analysis and determinations were made at least in duplicate. Endrin was extracted from the seed in Skellysolve B (n-hexane), and extracts were cleaned up of extracted fats, concentrated, and dried, essentially as outlined by Bann *et al.* (1958). Amounts of endrin in the extracts were determined by gas chromatography with an Aerograph Model 1840-1 instrument equipped with an electron capture detector and a 5 ft by ⅛ in I.D. glass column packed with 6 percent SE-30 on 80- to 100-mesh Varaport-30. Injector, column, and detector temperatures were 200°, 190°, and 200° C, respectively. Nitrogen was used as carrier gas at a flow rate of 40 ml per minute. Endrin was quantified by peak height, and data were appropriately corrected according to previously determined recovery efficiencies. Recovery percents were obtained from analyses of known quantities of endrin added to samples of untreated Douglas-fir seed, using Dow Latex 512-R as adhesive. To closely simulate actual treatments of the seed lots studied, aluminum powder and Monastral green were each added to one-half of the recovery samples in amounts comparable with those used by the different organizations.

Results

Efficiency of endrin recovery. Recovery of endrin added to the untreated seed samples did not vary with amount of endrin added or the coloring material used for identification. Thus, the average recovery of 85.0 percent, computed from data of 12 analyses, was used to correct all data shown in Figure 1.

Effect of treatment. Success of treatment, measured by endrin found on the seed as percent of endrin used as indicated by the participating organizations, differed

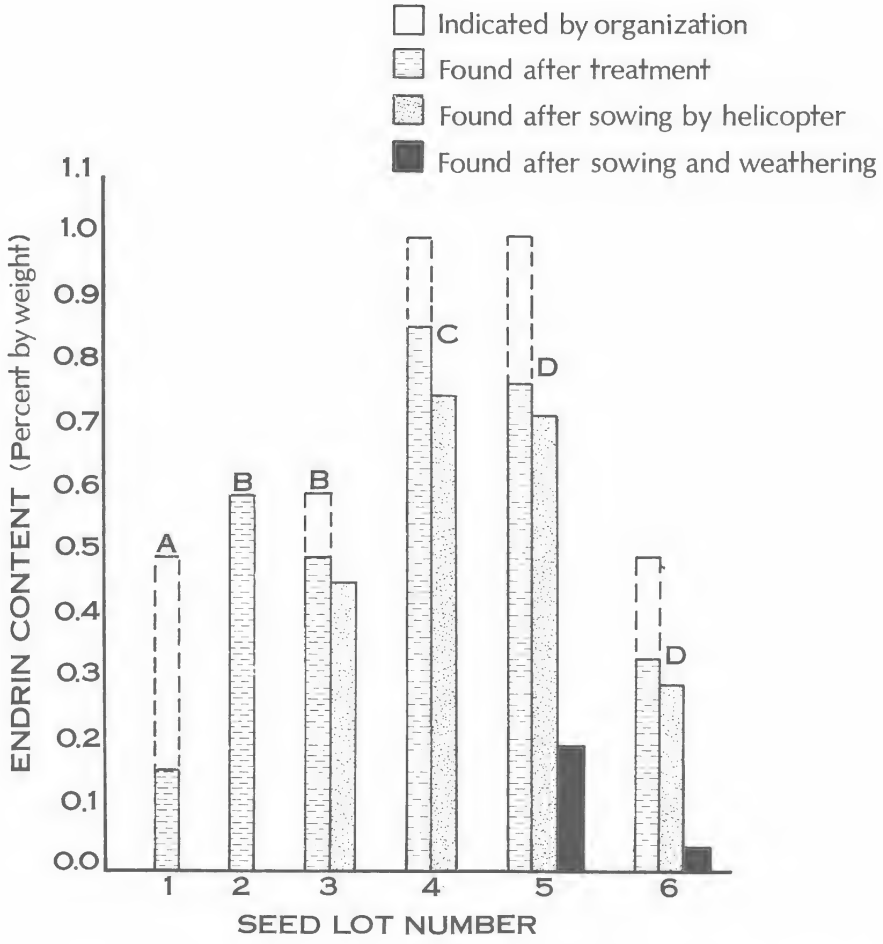

Figure 1. Endrin used in seed treatment as indicated by organization, and endrin found on treated seeds after treatment, sowing by helicopter, and after sowing and weathering. (Letters above bars identify participating organizations. Sowing was simulated in lots 3 and 4.)

among the treatments and was not consistent within seed lots of the same organization (Fig. 1). Thus, following treatment, endrin found on seeds of lots 1, 3, 4, 5, and 6 was less than the amounts indicated for the treatments. The difference varied among these lots; it was largest with lot 1, intermediate with lots 3, 5, and 6; and smallest with lot 4. Only seeds of lot 2 showed an endrin content equal to the theoretical value indicated.

Effect of sowing by helicopter. Aerial dissemination reduced the endrin content of the seed (Fig. 1). Reductions, however, were small, ranging from 4 to 17 percent of the original endrin, with little difference between actual and simulated seedings.

Effect of weathering. Losses of endrin caused by weathering were very large (Fig. 1).

After about three months of exposure in the field, seed of lots 5 and 6 lost 72 and 86 percent, respectively, of the endrin which was on the seeds after sowing. Thus, by May and still before full germination, only a very small fraction of the original endrin remained on this seed.

Discussion and Conclusions

Results show that endrin content of commercially treated Douglas-fir seed was affected by treatment, sowing by helicopter, and weathering. Following treatment, in all but one seed lot where probably more endrin than required was initially added, treated seed contained less endrin than the indicated amounts used. The endrin-coating method as originally proposed in 1956 (Anonymous, 1956) obviously does not allow application of all endrin to the seed. However, losses of endrin due to treatment in lots 1 and 6 appear excessive, and it is doubtful that seeds of these lots contained sufficient endrin for adequate protection from rodents (Radwan *et al.,* 1970).

Reductions of endrin content caused by aerial dissemination were small. These reductions, however, may be important when endrin content of the seed before sowing is already low. This was probably true in lots 3 and 6 where the combined effects of treatment and sowing reduced the endrin content of the seed to 0.46 and 0.29 percent, respectively.

Weathering caused the greatest endrin losses. It reduced the endrin on seeds of lots 5 and 6 tremendously and probably increased the vulnerability of the seeds to predation by rodents. Clearly, endrin was not adequately bound to the seeds by the adhesive used. Improvement of the endrin treatment by use of a higher concentration of the adhesive or another adhesive with better binding properties under the weathering conditions of the Pacific Northwest is, therefore, indicated. Alternatively, impregnation of seed with endrin would also minimize weathering losses.

The effects of treatment, sowing, and weathering on endrin content of Douglas-fir seed demonstrated here may partially explain observed reforestation failures with endrin-treated seed. Study results also show the importance of chemical analysis in evaluating endrin and indicate means for improving the treatment.

Concern over use of the "hard" pesticides dictates that endrin, a persistent chlorinated hydrocarbon, be eliminated as a seed protectant as soon as a more acceptable chemical becomes available. Fortunately, however, the chemical analysis approach used in this study can and should be employed together with the more common bioassay tests in evaluating candidate chemicals to replace endrin.

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Literature Cited

Anonymous. 1956. 1956 formulation for the treatment of coniferous tree seed. U.S. Fish and Wildl. Serv., Wildl. Res. Lab., Denver. 2 pp. (Spec. release.)

Bann, J. M., S. C. Lau, J. C. Potter, H. W. Johnson, Jr., A. E. O'Donnell, and F. T. Weiss. 1958. Determination of endrin in agriculture products and animal tissues. J. Agr. Food Chem. 6: 196-202.

Dick, J., J. M. Finnis, L. O. Hunt, and N. B. Kverno. 1958. Treatment of Douglas-fir seed to reduce loss to rodents. J. Forest. 56: 660-661.

Dimock, E. J., II. 1957. A comparison of two rodent repellents in broadcast seeding Douglas-fir. USDA Forest Serv., Pacific Northwest Forest & Range Exp. Sta. Res. Pap. 20. 17 pp.

Mann, W. F., Jr. 1968. Ten years' experience with direct-seeding in the South. J. Forest. 66: 828-833.
Radwan, M. A. 1969. Protection of coniferous seed from rodents. Ore. State Univ., Corvallis, Ore. Wildl. & Reforest. Symp. Proc. 1968: 52-54.
————, G. L. Crouch, and W. D. Ellis. 1970. Impregnating and coating with endrin to protect Douglas-fir seed from rodents. Pacific Northwest Forest & Range Exp. Sta., USDA Forest Serv. Res. Pap. PNW-94. 17 pp.
Roy, D. F. 1961. Seed spotting with endrin-treated Douglas-fir seed in northern California. USDA Forest Serv., Pacific Southwest Forest & Range Exp. Sta. Tech. Pap. 61. 12 pp.

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Biological Observations on Cobb Seamount

Information on benthic communities of seamounts is of ecological and biogeographical value because of their isolation by intervening deeper water from other communities at comparable depths. As is the case for terrestrial life on oceanic islands, seamounts can be expected to have unique biotic compositions. These underwater "islands" offer opportunities to study species interactions within biotic communities by investigating the success of familiar species in the absence of predators, competitors, or usual prey and in the presence of species to which they are not usually exposed. We can also examine the sort of characteristics possessed by species capable of colonizing and maintaining an isolated population. There are few published observations on the biota of seamounts and those that exist usually involve samples acquired by dredges or fishing gear (e.g., Powell *et al.,* 1952; Hubbs, 1959; Budinger and Enbysk, 1960).

I am reporting on some observations made on the Cobb Seamount which lies 270 miles west of Grays Harbor, Washington (46°44′N, 130°47′W). The physiography of Cobb Seamount is described by Budinger and Enbysk (1960). This underwater volcanic mountain rises from a depth of 3000 meters off the Cascadia Abyssal Plain to within 34 to 46 meters of the surface. The summit is a pinnacle rising from a terrace at 100 meters. The pinnacle top is approximately 880 meters long and 577 meters wide and is generally flat with small dips, gulches, pot holes and rises. I found no fracture lines nor any loose rocks. For all practical purposes, the top of Cobb Seamount seems to be one solid, stable mass. The only interstices available as shelter for crustaceans, annelids, etc., are those formed by the bases of attachment of sessile organisms (e.g., *Hinnites multirugosus* and *Phyllochaetopterus prolifica*).

This report presents a species list, some general observations, some speculations based on these observations, and some suggestions for future experiments or studies. The observations are founded on about 35 minutes of experience on the Cobb Seamount, some of which was devoted to other tasks. As all dives were made for purposes other than biological investigation, no quantitative data were collected. Three dives were made on the shallow (37 meter) northern side of the seamount during which 36 photographs were taken of the bottom to record, confirm, reconstruct, and extend our observations. These limitations should be taken into consideration when generalizing to the whole seamount.

Table 1 presents the species list compiled with the help of Richard E. Norris (algae), Phillip A. Lebednik (coralline algae), Rita Gustus (polychaetes), and Alan J. Kohn (gastropods) of the University of Washington; June R. P. Ross (ectoprocts) of Western Washington State College; Mary E. Rice (sipunculans) of the Smithsonian Institution; Josephine F. L. Hart (decapod crustaceans) of the University of Victoria;

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Michael A. Kyte (ophiuroids) of Oregon State University; and Charles R. Hitz and Benjamin Patten (fish) of the U.S. Bureau of Commercial Fisheries. Many species are still unidentified, including many amphipods and at least five species of conspicuous demosponge, and a chiton.

TABLE 1. Organisms identified from Cobb Seamount.

Chlorophyta
- *Pseudopringsheimia apiculata* Setchell & Gardner

Phaeophyta
- *Desmarestia viridis* (Müller) Lamouroux

Rhodophyta
- *Polysiphonia* (sp.)
- *Lithothamnion* (sp.)
- *Lithophyllum* (sp.)

Cnidaria
- *Metridium senile* (Linnaeus)
- *Corynactis californica* Carlgren
- *Cribrinopsis* (sp.)
- *Velella lata* Chamisso & Eysenhardt

Ctenophora
- *Beroë* (sp.)

Ectoprocta
- *Borgiola pustulosa* (Osburn)
- *Rhamphostomella spinigera* Lorenz
- *Felicrisia* (sp.)
- *Crisia* (sp.)

Mollusca
- *Hinnites multirugosus* (Gale)
- *Calliostoma ligatum* Gould
- *Margarites beringinsis* Smith (1 specimen only; identification tentative)
- *Homalopoma carpenteri* (Pilsbry)
- *Searlesia dira* (Reeve)
- *Fusitriton oregonensis* (Redfield)
- *Ocenebra lurida* (Middendorf)
- *Dirona albolineata* MacFarland
- *Archidoris montereyensis* (Cooper)
- *Archidoris* (= *Austrodoris*) *odhneri* MacFarland

Sipunculoidea
- *Phascolosoma agassizii* Keferstein

Annelida
- *Euphrosyne bicirrata* Johnson
- *Euphrosyne hortensis* Moore
- *Phyllodoce* (*Anaitides*) *maculata* Linnaeus
- *Trypanosyllis gemmipara* Johnson
- *Nereis procera* Eklers
- *Eunice kobiensis* McIntosh
- *Lumbrinereis* (sp.)
- *Phyllochaetopterus prolifica* Potts
- *Spirorbis* (sp.)
- *Serpula vermicularis* Linnaeus
- *Chitinopoma groenlandica* (Mörch)

Arthropoda
- *Lepas anatifera* (Linnaeus)
- *Pagurus cavimanus* (Miers)
- *Chorilia longipes* Dana

TABLE 1. (cont.)

Echinodermata
- *Pycnopodia helianthoides* (Brandt)
- *Orthasterias koehleri* (de Loriol)
- *Leptasterias hexactis* (Stimpson)
- *Henricia leviuscula* (Stimpson)
- *Crossaster papposus* (Linnaeus)
- *Axiognathus squamata* (Delle Chiaje)
- *Strongylocentrotus franciscanus* (Agassiz)

Chordata
- *Prionace glauca* (Linnaeus)
- *Sebastodes rubberrimus* Cramer
- *Sebastodes paucispinus* (Ayres)
- *Sebastodes entomelas* (Jordan & Gilbert)
- *Hemilepidotus spinosus* (Ayres)
- *Mola mola* (Linnaeus)

Different groups of animals were found on the horizontal and vertical surfaces. Although generally flat, the top of the seamount did have numerous shallow depressions, holes, or gulches with vertical sides. These vertical surfaces were almost entirely dominated by populations of *Hinnites multirugosus* (Fig. 1). The *Hinnites,* in turn, were covered with dense growths of *Phyllochaetopterus* tubes, sponges, bryozoans, and *Corynactis* and *Metridium.* Thus, vertical surfaces were covered two layers thick with sessile organisms. It is especially interesting that *Hinnites* takes over the entire primary substratum on these surfaces since, in my experience, it always shows a scattered distribution in other areas of the Northeast Pacific.

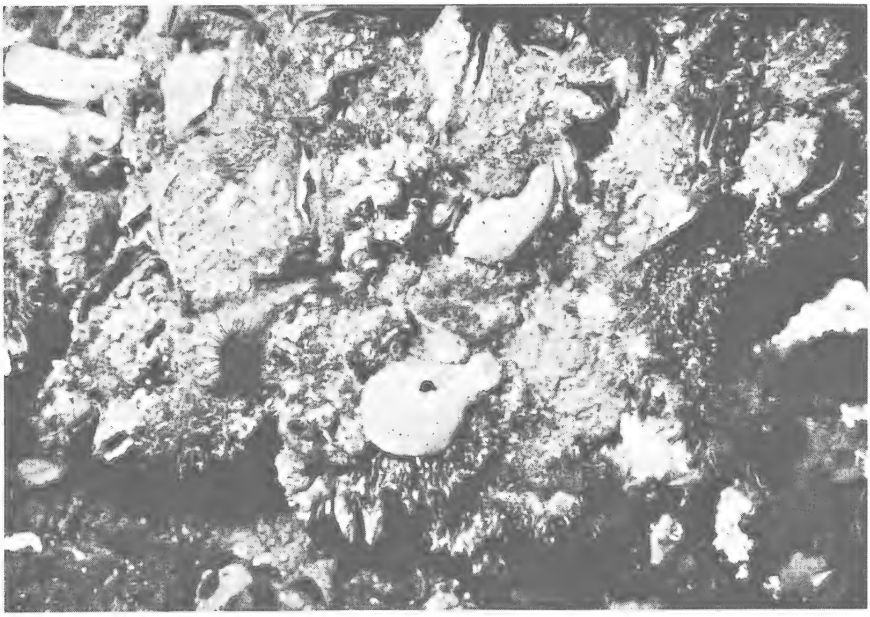

Figure 1. Fauna encrusting vertical surfaces on the top of Cobb Seamount. Gaping apertures from a nearly continuous layer of rock scallops are apparent beneath an upper layer of sponges, tube worms, and anemones.

The relative abundance of *Hinnites* may be causally related to the relative scarcity of *Orthasterias koehleri. Orthasterias* is probably the only predator of adult *Hinnites* on the Cobb Seamount. This seastar has been seen preying on *Hinnites* on the outer coast of Washington, and Spencer Campbell and Roland White (personal communications) saw an *Orthasterias* eating a *Hinnites* on the Cobb Seamount. *Orthasterias* seems to be fairly scarce ($<1/2000$ m^2) although the individuals we did see were very large (about 0.6 m in diameter). Why *Orthasterias* is scarce is unknown. It has a planktonic larval stage as do *Pycnopodia* and *Henricia,* which are common on the seamount. The major source of food for very small *Orthasterias,* chitons and small snails, is plentiful.

The horizontal surfaces were characterized by a very different biota (Fig. 2).

Figure 2. Fauna occupying the horizontal surfaces on the pinnacle of Cobb Seamount. Anemones (*Metridium*), urchins (*Strongylocentrotus*), and top shells (*Calliostoma*) are seen on a substratum of coralline algae.

The rock substratum was covered with either of two types of coralline algae (*Lithothamnion* sp. and *Lithophyllum* sp.). I saw no bare rock surface where we dived. The encrusting fauna grew over this base of coralline algae. Large patches of thin, bright red, encrusting demosponge grew and even predominated in some areas. A purple calcareous encrusting bryozoan (*Borgiola pustulosa*) was predominant in other areas. A yellow didemnid colonial tunicate, the fluorescent crimson *Corynactis,* and scattered *Metridium* were all abundant. Occasional clumps of *Phyllochaetopterus* tube worms provided interstices for sipunculans, caprellids and other amphipods, and many polychaetes. The filamentous algae, *Desmarestia* and *Polysiphonia,* were commonly growing out of small depressions. In general, the variety of life was greatly reduced from that expected on a comparable area of basalt on the mainland. However, those

species present all seemed to be abundant, and species diversity would be high if evaluated on a "number of individuals per species" basis.

Many of the animals found on the seamount are usually limited in distribution to the intertidal or very shallow subtidal. Examples are *Leptasterias hexactis, Homalopoma carpenteri, Searlesia dira,* and *Phascolosoma agassizii.* That these animals survive well at 37 to 40 m depths on top of the seamount indicates that they are not restricted to the intertidal by the demands of their own physiology. Rather, they are probably prevented from exploiting the deeper habitats by predators, competitors, or other animals.

An alga, *Pseudopringsheimia apiculata,* and an anemone, *Corynactis californica,* have not been previously reported from Washington. They are typically from California. This range extension may be caused by the water over the seamount being somewhat warmer than the water closer to the coast. The prevailing current is from the northwest.

There may be some endemism among the animals of Cobb Seamount. Alan J. Kohn (personal communication) notes that the most common gastropods on the seamount, *Calliostoma ligatum,* "have lower length/width ratios than Mukkaw Bay specimens and the light tan transverse lines are smooth, not raised riblets." The *Strongylocentrotus franciscanus* urchin population also differs slightly from those around the state of Washington. Two color phases, red and purple, are both common about the mainland. I saw only purple individuals on the seamount. Further, the Cobb Seamount *S. franciscanus* had a habit of holding bits of shell or coralline algae over themselves. I have never seen *S. franciscanus* do this before, although *S. purpuratus* does it regularly.

Strongylocentrotus franciscanus is the most conspicuous animal on Cobb Seamount. Its average abundance was estimated at 2.6/m^2. The estimate is based on a count of urchins in 1234 m^2 from videotape recordings of transects across the seamount made by Walter C. Sands (Department of Oceanography, University of Washington) in May and June of 1965. A major predator of *S. franciscanus, Pycnopodia helianthoides,* is also very common. An average of one *Pycnopodia* per 140 m^2 was estimated from videotape recordings of 2520 m^2. If we assume the incidence of feeding by *Pycnopodia* on urchins on the Cobb Seamount to be roughly 50 percent, similar to that of *Pycnopodia* on urchins on the outer coast of Washington (Mauzey *et al.*, 1968), and if we assume that digestion of an adult urchin takes approximately 48 hrs (Greer, 1961), then each *Pycnopodia* would eat about 90 adult urchins per year. Thus, *Pycnopodia* predation may take 25 percent of the standing crop of adult urchins. This could be a significant mortality factor for these long-lived animals.

The urchins, in turn, may be responsible for the nature of the algae on the seamount. The only common algae, other than corallines, were filamentous forms, predominantly *Desmarestia viridis* and *Polysiphonia. Desmarestia* is remarkable for its acidity, which probably serves as an antiherbivore device. Paine and Vadas (1969) have shown experimentally that *Polysiphonia* will coexist with urchins even though the urchins have removed most of the other algae. There are a few very tiny leafy red algae on the rock scallop shells, but these are probably kept scarce by the grazing of the abundant urchins, which would not eat *Desmarestia* nor *Polysiphonia* until most of the leafy reds were gone. Peter B. Taylor (personal communication), on an earlier expedition, saw a patch of kelp or large leafy brown algae while being towed

across the seamount 13 m above its surface. However, there seemed to be few or no urchins in this region. To test whether low light intensities or urchin grazing are responsible for the sparse algal flora, urchins could be excluded by placing small cages on the seamount.

Metridium senile, a suspension feeding anemone, was very common on the seamount, but I never saw any large individuals (greater than 30 cm tall). Further, the *Metridium* seemed to tend toward the same medium size (between 10 and 20 cm tall). To find whether this uniform medium size is not due to a particularly successful recruitment in the recent past but to a relatively low supply of suspended matter acceptable as food to *Metridium,* it would be interesting to take a few of the large *Metridium* from Puget Sound and set them in a cage on the seamount. If these large *Metridium* eventually shrank to a size comparable to that of the resident population, it might indicate that the relatively reduced size is what can be maintained, given the available food. Perhaps *Metridium* size distributions could be used as an indicator of the amount of available suspended matter appropriate as food.

A particularly interesting find was the abundance of the brooding starfish, *Leptasterias.* It does not have a planktonic larval stage, yet it is inconceivable that it could have crawled the 270 miles across the abyssal plain. However, we saw *Nereocystis* and driftwood floating over the seamount, and *Leptasterias* often crawls up on kelp in pursuit of small snails. *Searlesia dira* is another species which is common on the seamount and which has no planktonic stage in its life history. It hatches directly as a young snail from an egg capsule attached to a hard (usually rock) substratum. Dispersion is thought to be one of the benefits of the more "wasteful" planktonic larva, but species which brood their offspring seem to have a high probability of successful recruitment of small isolated areas, given enough time.

Once on the seamount, a brooding species might have an advantage in maintaining a population. Planktonic larvae would tend to be swept out to sea. Species with planktonic larvae, however, also seem to be characterized by successful recruitment. An abundant set of *Hinnites* was evidenced by large numbers of individuals 2.3 to 5.5 mm long. These were found in interstices of *Phyllochaetopterus* tubes, attached to the tubes or to sponges. Similarly, a large number of small (about 4 cm diameter) and medium-sized (about 8 cm diameter) *Strongylocentrotus franciscanus* were found. In fact, the size distribution of *S. franciscanus* was far more even than in the San Juan Islands, where adults tend to predominate. The relatively high rate of *Pycnopodia* predation may reduce the proportion of adult urchins. With a higher mortality of adults, the young may have less competition.

Hydroids and barnacles are generally very successful colonizers, so both were especially conspicuous by their absence. Not a single hydroid or barnacle has ever been seen on Cobb Seamount. The small yellow didemnids were the only tunicates found. In contrast, tunicates are one of the predominate groups of subtidal space holders in rocky areas on the Washington coast.

Another seamount which rises to within diving distance of the surface has been found in the Northeast Pacific (Scrimger and Bird, 1969). This is the Bowie Seamount which lies about 120 miles west of the Queen Charlotte Islands and rises to within 30 meters of the surface. The lists of species from Cobb Seamount (this paper) and from Bowie Seamount (Scrimger and Bird, 1969) have surprisingly little in common. Barnacles (*Balanus nubilus*), hydroids (*Obelia* sp.), and holo-

thurians (*Eupentacta quinquesemita*) were all found on Bowie Seamount. *Mytilus californianus* and *Saxicava pholadis* were found on Bowie, whereas *Hinnites multirugosus* was the predominant bivalve on Cobb. The starfish *Pycnopodia helianthoides* and *Henricia leviuscula* were common to both seamounts.

The placement of instrument packages, beacons, sound pingers, and buoys on seamounts provides an excellent opportunity to index the population of planktonic larvae of sessile organisms far at sea. These objects are emplaced on known dates, so rates of settlement and invasion as well as growth rates of sessile organisms may be compared with those rates on similar objects nearer the mainland. As samples of rock are blasted from the surface of the seamount, bare patches are left on the spot from which the sample was removed. These bare spots are created on a known date and can thus provide a source of similar information on a substratum which is more natural than the instrument packages. The beacons, pingers, and buoys further provide the ability to relocate particular spots on the seamount. This is essential for relocation of cages, rock sample areas, and other experiments.

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Literature Cited

Budinger, T. F., and B. J. Enbysk. 1960. Cobb Seamount, a deep-sea feature off the Washington Coast. Department of Oceanography, University of Washington Technical Report No. 60.

Greer, D. L. 1961. Feeding behavior and morphology of the digestive system of the sea star *Pycnopodia helianthoides* (Brandt) Stimpson. Master's thesis, University of Washington.

Hubbs, C. L. 1959. Initial discoveries of fish faunas on seamounts and offshore banks in the Eastern Pacific. Pac. Sci. 13(4): 311-316.

Mauzey, K. P., C. Birkeland, and P. K. Dayton. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. Ecol. 49(4): 603-619.

Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins *Strongylocentrotus* spp., on benthic algal populations. Limnol. & Oceanog. 14(5): 710-719.

Powell, D. E., P. L. Alverson, and R. Livingstone. 1952. North Pacific Albacore Tuna Exploration. 1950. Fish and Wildlife Service, U.S. Department of the Interior, Fishery Leaflet 402, pp. 45-55.

Scrimger, J. A., and J. Bird. 1969. Bowie Seamount—preliminary survey for instrument package placement. Defense Research Board of Canada Tech. Mem. 69-7.

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The Effect of Spray Irrigation on Plum Temperatures[1]

The Early Milton variety of the Italian prune plum (*Prunus domestica*) has been extensively planted in Oregon because it ripens early in the season. Unfortunately, the fruit of this variety also tends to spoil rapidly after harvest. This spoilage appears related to excessive temperature of fruit during the growing season. The pulp of affected fruit first turns brown around the stone, which degrades its quality; decomposition and spoilage occur soon thereafter. Marketing of Oregon's Early Milton plum crop has been adversely affected by this internal browning.

One possible solution to the browning may be a reduction of orchard temperatures by spray irrigation during the warmer portions of the summer. We report on a test of spray treatment designed to modify the temperature regime of ripening plums in late August, about two weeks before harvest. The specific objectives of the test were to measure the maximum temperatures that naturally occur in the plums and to determine what changes in temperature result from spray cooling.

Experimental Method

The experimental area was near the center of the Willamette Valley, a broad, fertile agricultural area at an elevation of several hundred feet, with the Cascade Mountains to the east and the Coast Range to the west. The summer climate is characteristically mild and dry, and irrigation is widely practiced. Daily temperatures in Corvallis during August average around 28° C maximum and 10° C minimum. Maximum temperatures occasionally surpass 35° C, however. High intensities of solar radiation can occur in this dry, clear, summer climate; totals in August frequently reach 600 langleys per day.

A simple modification of the microclimate was accomplished by application of water, as mist, to a portion of a two-acre demonstration orchard near Corvallis. Mist nozzles were mounted above the crowns of eight adjacent trees in a two-row by four-row grid. Water was applied during the afternoons of warm days throughout the summer. The nozzle arrangement is shown in Figure 1. The mist was applied at a low rate, about 10 to 15 mm per hour. The small quantity, droplet size, and frequency of the mist treatment thus differed from conventional spray irrigation. The water, pumped from deep wells, had a constant 12° C temperature. The untreated trees in the orchard received normal irrigation as required during the summer.

[1] Paper 728, Forest Research Laboratory, School of Forestry, Oregon State University, Corvallis, Oregon.

Figure 1. Mist nozzle above an Italian prune plum in the left foreground. Recorder trailer is in the center.

Plum temperatures were sampled on two of the sprinkled trees and on two of the untreated trees. Four representative plums were selected on each of the four trees, two "sunny" plums on the south, and two "shady" plums on the north side of the crown. Exposure of the sampled plums was typical of other plums on the same side of the crown. A sample sunny plum is illustrated in Figure 2. Because of the leafy growth habitat of the Italian prune plum, even the sunny plums were shaded sometime during the day. Conversely, the normally shady plums occasionally received direct-beam solar radiation for short periods. The sampled fruit thus totaled 16 plums, eight on dry trees and eight on wet trees, with half of each treatment group on the sunny side and half on the shady side of the crowns. There were, then, four conditions for comparison: sunny dry, sunny wet, shady dry, and shady wet.

Air temperatures were measured at a height of 2 meters in two orchard locations. Dry ambient temperatures were taken in the center of an unsprinkled canopy; wet ambient temperatures in the center of a sprinkled canopy. The air temperature sensors, although already shaded by the canopy, were further protected against radiation and water by simple, nonaspirated shields. Plum temperatures were measured at the plum pit.

All temperatures were measured with 30-gauge copper-constantan thermocouples, referenced against a heated (65° C) junction. Data from the thermocouples were recorded on punched paper-tape at intervals of 10 minutes during the day and 20 minutes at night. The multichannel digital data-acquisition system[2] had an absolute accuracy of 2 microvolts (0.05° C). The temperature of an ice bath was also recorded

[2] Vidar Corporation, 77 Ortega Avenue, Mountain View, California 94040.

as a continuing check on the stability and accuracy of the entire temperature system. This check measurement indicated that the absolute accuracy of temperatures was better than 0.1° C, a precision considerably greater than that required for the following analysis.

Figure 2. Typical exposure of a plum on the south side of the crown. Copper-constantan 30-gauge thermocouples were used to measure temperatures at the center of the fruit.

Results

The measurements disclosed a characteristic temperature regime within the orchard. The plum and air temperatures were always in near equality (0.5° C or less) around midnight regardless of aspect or treatment. The temperatures began to diverge among plums and in the air soon after sunrise; no residual effects were apparent from the previous day's treatment. The mist application, which began about noon on most days, produced a marked cooling effect on the air and plums in the treated portion of the orchard. Temperature differences were also associated with aspect, or exposure, of plums. Shady plums were always cooler than those on the sunny side of the same crown.

The temperature regime of the plums was thus affected by treatment and by exposure. The effects can be illustrated by considering the heating and cooling cycles throughout one of the warmer sample days (August 22, 1967). Observations at the Corvallis agricultural weather station showed that the maximum temperature was 32.8° C and winds were light, averaging a little over 3 km per hour during the day. Skies were clear except for a small amount of haze between 1300 and 1400 hours, Pacific Daylight Time (PDT), and solar radiation totaled 590 langleys for the day. True solar time was 1 hour and 50 minutes behind PDT on this date.

Observations within the untreated (dry) portion of the orchard will be presented

first. The maximum air temperature was 31.3° C at 1720 PDT, about 3½ hours after true solar noon. The early morning minimum was 11° C. The mean hourly temperatures of air and plums are plotted in Figure 3 for the untreated portion of the orchard. In addition, the maximum and minimum plum temperatures observed at each sample time are plotted individually. The maximum temperatures were always associated with sunny plums and minimum temperatures with shady plums. Thus the spread between maximum and minimum values illustrates the extreme effects of aspect. Figure 3 shows that dry shady plums remained close to air temperature, but dry sunny plums rose well above air temperature. The maximum plum temperature of 41.3° C occurred at the time of the maximum air temperature (31.3° C). The temperatures of the dry sunny plums fell during the early evening and approached the values of the air and the shady plums. Figure 3 shows a small dip in maximum plum temperatures in the early afternoon; this was associated with the small amount of haze that temporarily marred the otherwise clear day.

Observations within the treated (wet) portion of the orchard will be considered next. The effect of the spray treatment on the temperature regime of the treated plums is shown in Figure 4. The cooling effect of the spray cycle that began at 1140 PDT and ended at 1500 PDT is clearly evident. The mean temperatures of the sprinkled fruit, in both sun and shade, dropped 3° C soon after sprinkling began. The mean temperatures of the sprinkled fruit stabilized about 5° C lower than the unsprinkled fruit of similar exposure. Examination of the individual measurements revealed that about 15 minutes was required for a plum to achieve two-thirds of the imposed change in temperature.

Figure 4 shows that the effects of sprinkling are apparent for several hours after

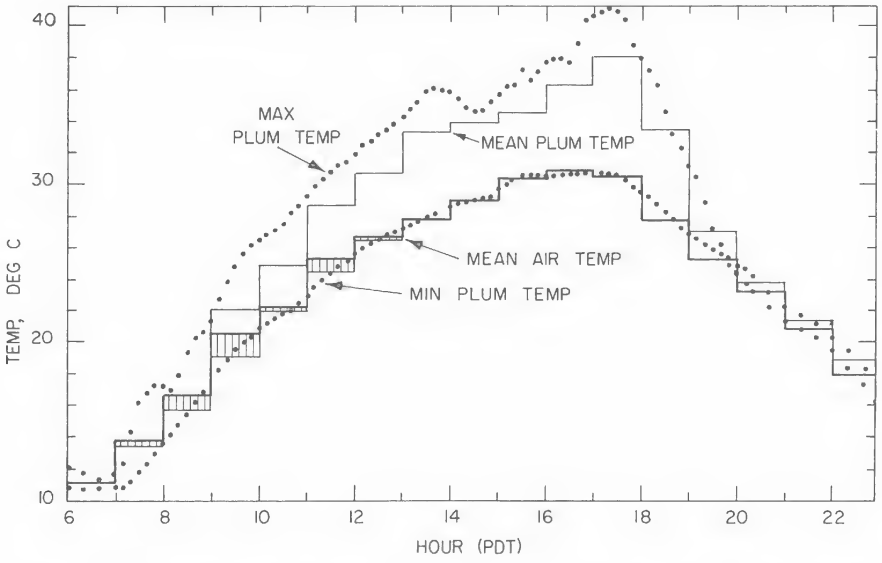

Figure 3. Effects of aspect on temperatures of unsprinkled plums. Maximum (upper dots) and mean (upper line) temperatures of sunny plums, mean air temperature (heavy line), and minimum temperature of shady plums (lower dots). Mean temperature of shady plums is shown only when it was below the air temperature.

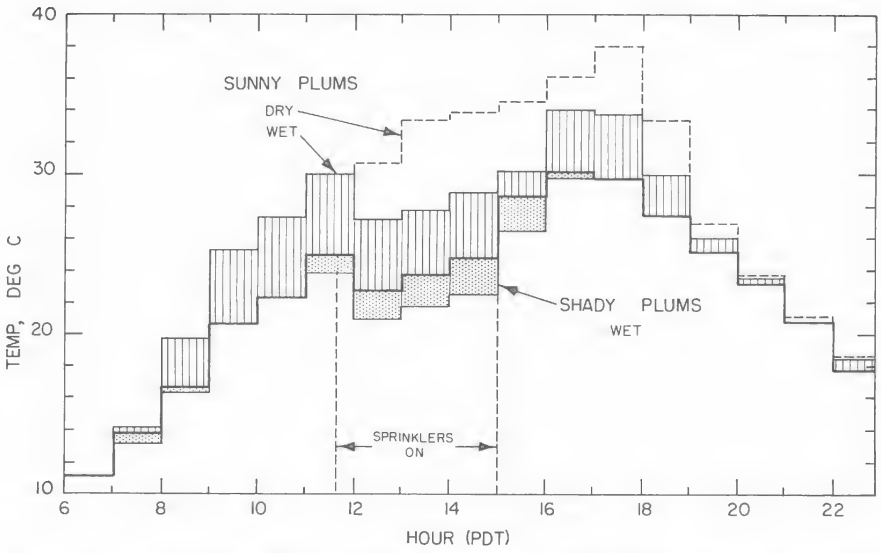

Figure 4. Effects of sprinkling on temperatures of plums. Mean temperatures of sunny plums, unsprinkled (dry) and sprinkled (wet), and mean air temperature (heavy line). Mean temperature of shady plums is shown when it was below air temperature (bottom line). Mean temperature of shady unsprinkled plums is not shown after sprinkling started.

treatment ceased. This is most noticeable for the sunny plums, as the treated sunny plums remained about 4° C cooler than the dry sunny plums until late in the evening, well after sprinkling ceased.

As an example of the contrast in temperature created by the spray, the maximum difference at any one time between a wet shady plum and a dry sunny plum was 15.8° C. The difference between the means of the dry sunny plums and the wet shady plums for the hour centered on 1430 was 11.5° C. During this hour, the four dry sunny plums averaged 33.8° C, the four wet sunny plums averaged 27.6° C, and the four wet shady plums averaged 22.3° C (Table 1). The effects of shade alone are also noticeable; the dry shady plums averaged 29.4 C. These values demonstrate that substantial modification of the microclimate can be achieved in orchards by mist application of water.

Discussion

Because the average temperatures of the treated plums were observed to be about 6° cooler than the untreated plums during the treatment period, the experiment clearly indicates that substantial cooling can occur as a result of sprinkling. A complete development of the effects of the water on the energy balance of the plums would require more data than were obtained in this preliminary study. The observed temperatures can provide a basis for speculation regarding the nature of the cooling process, however. A discussion of the cooling process should be of value in planning subsequent studies of orchard climate.

The observed temperatures represent the amount of thermal energy that results from the relative effectiveness of the various modes of transfer of energy between the

TABLE 1. Hourly means of plum and air temperatures (°C) on August 22, 1967. Spray cycle in operation from 1140-1500 PDT. Sampling design explained in text.

	Sunny plums		Shady plums		Air	
Hour	Dry	Wet	Dry	Wet	Dry	Wet
7	12.6	14.2	13.7	13.4	13.9	14.3
8	16.6	19.9	15.9	16.9	16.7	17.3
9	22.1	25.4	19.4	20.5	20.7	20.3
10	24.9	27.4	22.2	22.1	22.4	22.1
11	28.5	30.1	24.5	24.0	25.3	23.9
12	30.7	27.3	26.5	21.3	26.7	22.7
13	33.2	27.6	28.4	22.0	27.8	23.8
14	33.8	27.6	29.4	22.3	29.0	24.9
15	34.4	30.0	30.4	26.5	30.4	28.7
16	36.2	34.0	31.1	29.9	30.7	30.2
17	38.0	33.6	31.1	30.8	30.4	29.8
18	33.4	29.9	29.0	29.8	27.8	27.4
19	27.2	26.0	26.3	26.6	25.1	25.0

plums and the environment. Two transfer processes of major importance can be identified as operating on both the treated and untreated plums: convection between the plums and the air, and net exchange of short- and long-wave radiation between the plums and their surroundings. Two additional processes, evaporation and conduction, operate only on the treated plums. The wet plums will dissipate additional energy as water evaporates from their surface. The wet plums may also lose energy by conduction into the cool water that falls on them.

There is a change in stored energy as the plums heat or cool. This change in storage may also be considered as an energy-transfer process. The amount of energy involved is a function of the temperature and the heat capacity of the plums. The energy transferred can be neglected and the analysis simplified by selecting periods in which steady-state conditions prevail. For the purpose of this discussion, the period 1200-1500 PDT satisfactorily approximates a steady state in which the changes in temperature and stored energy are small.

An examination of the convection process can provide some interesting insights into the nature of the observed plum cooling. Convection (Q, cal/cm^{2}min) between a body and the surrounding air is commonly expressed (Gates, 1962, Chapter 4) as:

$$Q = -h_c\ (T_{fr} - T_a) \qquad (1)$$

Equation 1 assumes that the convection flux is directly proportional to the temperature difference ($T_{fr} - T_a$) between the fruit and the air at a point where T_a is unaffected by the variations in T_{fr}. The constant of proportionality (h_c) is generally called the convective heat transfer coefficient. Because this coefficient is a function of fruit size, shape, and wind speed, it must be equal for all fruit of the same size exposed to the same air movement. Thus, among the sampled fruit in this study, h_c will be considered equal for all fruit with the same exposure, either among all

sunny plums or among all shady plums, regardless of spray treatment application.

The deviations of fruit temperatures from that of the air can be related to convective exchange as given by Equation 1. The temperatures needed in the equation are shown in Figure 5 as mean hourly deviations of dry plum temperature from that of the dry air and of wet plum temperature from that of the wet air.

Patterns in the temperature relations become apparent when the data are plotted in Figure 5 as deviations in temperature of dry and wet plums from the respective temperatures of dry or wet air. For example, during the spray period, the sunny dry plums remained about 5° C above dry ambient temperature, and the sunny wet plums were about 4° C above wet ambient temperature. The shady dry plums were just at air temperature during this period, but the shady wet plums dropped about 2.5° C below wet ambient temperature. Thus, the temperatures of both the dry and the wet plums have a certain similarity in their relation to the respective air

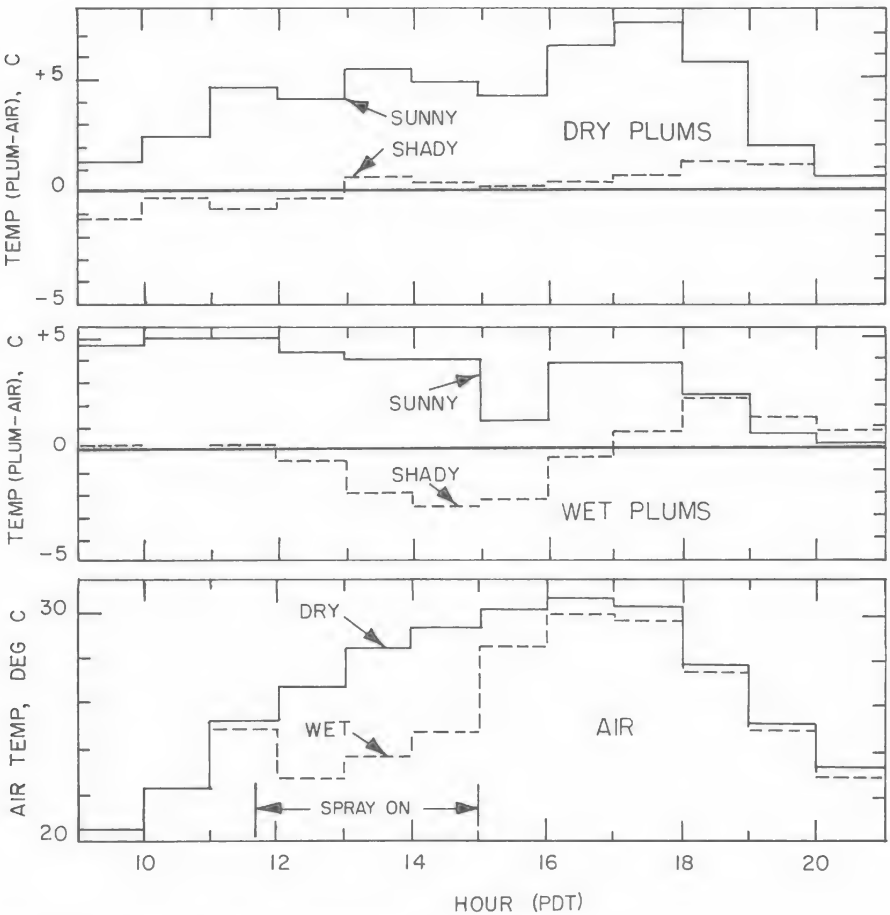

Figure 5. Deviations of plum temperatures from air temperatures.

temperature. This similarity is evident even though the average dry and wet air temperatures differed by as much as 5° C.

Equation 1 can now be used with the temperature difference data to estimate the relative magnitude of the convective flux for each group of plums with similar exposure. Let us consider first the sunny plums. Equation 1 predicts that the convective flux between the dry sunny plums and the surrounding air is related to the wet sunny plums by the ratio of their respective deviations from air temperature

$$Q_{wet}/Q_{dry} = (T_{wet} - T_{wet})/(T_{dry} - T_{dry}) = 4°/5° = 0.8 \qquad (2)$$
$$sun \quad sun \qquad fr \quad air \qquad fr \quad air$$

We interpret the unexpected similarity of the respective differences in fruit-air temperature as evidence that the convective flux was close to the same on both wet and dry sunny plums.

To proceed, we must consider net radiant heat flux available to the dry plums in relation to that supplied to the wet plums. In the absence of specific flux measurements, we shall assume relative equality of absorbed radiation. Such an assumption requires that the albedo of the wet plums be equal to that of the dry plums. In addition, the net exchange of long-wave radiation between the wet plums and their cooled environment must be about equal to that between dry plums and their warm environment.

Because of near equality of the convective fluxes on the wet and the dry sunny plums, the cooling efforts of the other energy transfer processes must have been relatively ineffective. This conclusion can be drawn if no additional energy source, such as increased radiation absorption, was available to the wet plums. Evaporation from the wet plum surface could not have contributed greatly to the cooling associated with spray treatment if the convective flux remained essentially unchanged. Conduction of energy from the plums into the cool (12° C or less) water falling on the fruit was also unimportant. Despite the combined effects of evaporation, conduction into the cool water, and convection, the temperature of the wet sunny plums still rose about 4° C above that of the wet air. In the dry plums, when convection was the only important cooling mechanism, the temperature rose about 5° C above the dry air temperature.

The mean temperature of the wet sunny plums averaged 5° C less than that of dry sunny plums. Our analysis indicates that about 1° C of this observed cooling could be attributed to the combined effects of evaporation and conduction of energy into the cool water. The surprisingly small effect of evaporation and conduction presumably is related to near-saturation of the air in the sprayed portion of the orchard, and to the small quantity of water (about 10-15 mm/hr) estimated to fall directly on the fruit.

If the previous assumptions of equal convection coefficients and lack of additional energy source for evaporation also apply to the shady plum observations, then, apparently, evaporation and convection together were able to lower the wet plum temperatures about 2.5° C below that of the wet air. The shady dry plums remained at the dry air temperature. Because the treated fruit averaged 6.5° C less than the untreated fruit, the major cooling again appears related to the convective exchange between the dry or wet fruit and the respective dry or wet ambient air temperature.

Summary

Eight trees in an Early Milton plum orchard in western Oregon were cooled by spraying each afternoon throughout the summer in an attempt to reduce the heat damage that has frequently been observed in the fruit of this species. This study reports temperature contrasts observed between sprinkled plums and unsprinkled controls during afternoon spray periods in late August, 1967. The air temperatures in the control portion of the orchard averaged about 30° C. The measurements, obtained at the plum pit with fine-wire thermocouples, are referenced to the ambient air temperature in the control portion of the orchard.

Fruit on sprinkled trees typically averaged about 4° C below and fruit on control trees averaged about 3° C above dry ambient temperature. These averages do not reveal the important role of exposure in the plum temperature regimes. Plums on the shaded north side were about 6° C cooler than dry ambient temperature when sprinkled, but were about 1° C warmer than dry ambient temperature if unsprinkled. Plums on the exposed south sides remained just below dry ambient temperature when sprinkled, but were about 5° C warmer if unsprinkled. Sprinkling reduced plum temperatures by 5° to 7° C for similar exposures.

Consideration of the plum energy balance suggests that convection between the sprinkled plums and the evaporatively cooled orchard air provided most of the observed cooling. Conduction of energy into the cool water and evaporation at the plum surface appeared to play a minor role in the cooling process.

Light mist applications of water may therefore achieve desired cooling more effectively than heavier applications with conventional sprinkler irrigation. Such knowledge should assist in the development of special purpose irrigation systems. Overhead sprinkler systems may ultimately prove useful for heat control in summer in addition to their primary purpose of protection from spring frost.

Acknowledgement

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Literature Cited

Gates, D. M. 1962. Energy exchange in the biosphere. Harper and Row. New York.

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Psychrometric Determination of Water Potential of Desert Plants

Thermocouple psychrometry is increasingly being used for measurement of leaf water potential in the range of 0 to –50 bars on mesophytes (Boyer, 1968; Campbell *et al.,* 1966; Lambert and Schilfgaarde, 1965; Rawlins *et al.,* 1968). However, technical problems of measurement have prevented extension of such measurements to xerophytes at large potentials so that data on these most interesting plants are lacking. To obtain these measurements, a Spanner (1951) thermocouple psychrometer was employed. The thermocouple range was extended to about –100 bars with special welded thermocouples (Campbell *et al.,* 1968) and increased cooling time. Using the extended psychrometer range, leaf water potentials for native plants on the Arid Land Ecology Reserve of the U.S. Atomic Energy Commission's Hanford Reservation in south-central Washington were measured. The area is characterized by a semi-arid climate. The annual precipitation is 6.6 inches with annual relative humidity of 52 percent. Moderate to high winds are frequent throughout the year.

Materials and Methods

Leaf samples from native plants were collected, quickly put into a sample changer housing a microthermocouple (Campbell *et al.,* 1966), and the assembly placed in a water bath at 25°C. After the leaf had come to equilibrium with its environment, current was passed through the chromel-constantan thermocouple and, by Peltier cooling, a film of moisture condensed on the thermocouple. On disconnecting the current source, the measured thermocouple EMF, when compared with the dry reference junction, gave a measure of water potential or relative humidity of the tested sample. Standard reference curves (Fig. 1) relating water potential with EMF were previously obtained from standard KCl solutions.

Leaf water potentials of several plants are compared from collections made between September 21 and November 13, 1967. Leaf samples for each species were collected from the same plant, except for salt grass and watercress, which were taken from the same general location. Water contents of the collected leaf samples from sagebrush (*Artemisia tridentata*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus nauseosus*), and willow (*Salix* spp.) were gravimetrically measured in duplicate.

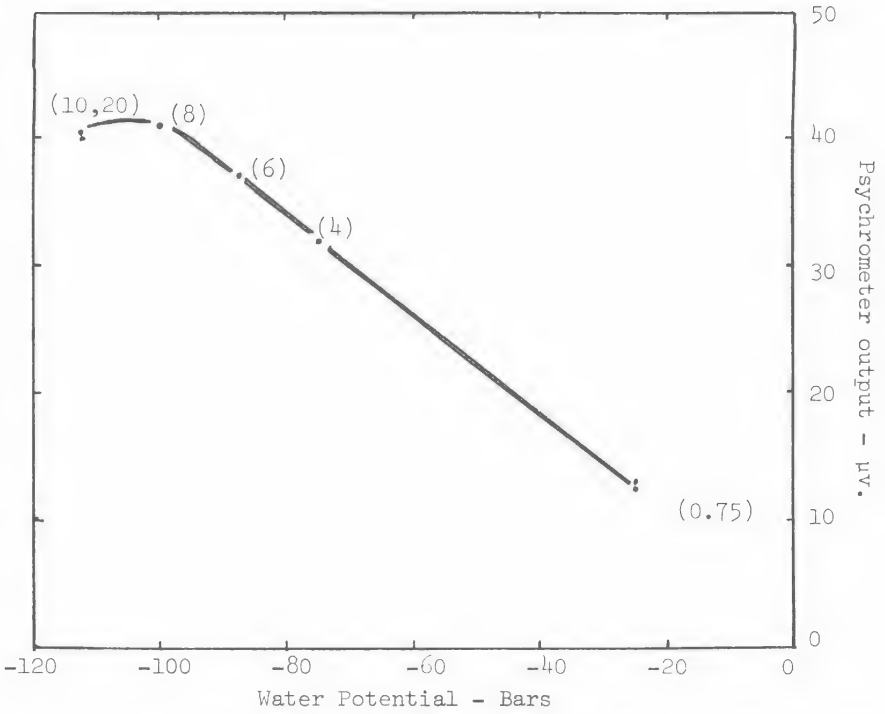

Figure 1. Calibration curve for Spanner psychrometer at 25°C, using long cooling times. Cooling current was 5 MA. Cooling time in minutes is shown in parentheses next to each experimental point.

TABLE 1. Comparison of leaf water potentials of desert plants at 8:30 a.m. and 1:15 p.m. on September 21, 1967

	Water Potential in –bars*	
	8:30 a.m.	1:15 p.m.
Sagebrush (*Artemisia tridentata*)	–44	–55
Greasewood (*Sarcobatus vermiculatus*)		
Whole leaf	–33	–38
Cut sections	–31	–35
Rabbitbrush (*Chrysothamnus nauseosus*)	–26	–32
Willow (*Salix* spp.)	–20	–28
*Climatic Conditions***		
Temperature, °C	19	31
Relative humidity, %	54	29
Cumulative radiation for day on horizontal surface, langleys	421	
Fraction of total radiation expected, %	89	
High and low 24 hour temperatures, °C	37,14	
Average wind speed at 50 ft, mph	7	
Sky cover from sunrise to sunset	0	

* –25.3 bar KCl standard solution, –24.5 bars measured.
** Data from Hanford Meteorology Station, Battelle-Northwest Laboratory, near sample locations.

TABLE 2. Comparison of leaf water potentials of desert plants in September and November and data on an aquatic plant in Rattlesnake Springs which winds through the desert of Hanford Reservation.

	Water Potential in –bars*				Leaf Water Content	
	8:30 a.m. Sept. 21	9:00 a.m. Sept. 25	9:00 a.m. Sept. 29	9:00 a.m. Nov. 13	Nov. 13 (dup. values) %	
Sagebrush (*Artemisia tridentata*)						
ca. 300 ft from Rattlesnake Spring	–44	–60	------	–43	112,	111
ca. 30 ft from Rattlesnake Spring	------	–62	------	–45	142,	141
Greasewood (*Sarcobatus vermiculatus*)	–33	–44	------	–37	397,	335
Rabbitbrush (*Chrysothamnus nauseosus*)						
ca. 400 ft from Rattlesnake Spring	–26	------	------	–27	88,	92
ca. 30 ft from Rattlesnake Spring	------	–33	------	–28	94,	93
Saltgrass (*Distichlis stricta*)	------	–94	------	–40	95,	91
Willow (*Salix* spp.)	–20	------	------	------	------	------
Watercress (*Nasturtium officinale*)						
Leaves (above water)	------	------	–18.5	–11	------	------
Buds of young leaves and stem (above water)	------	------	–15	------	------	------
*Climatic Conditions***						
Temperature, °C	19	23	24	10		
Relative humidity, %	54	40	34	76		
Cumulative radiation for day on horizontal surfaces, langleys	421	400	253	63		
Fraction of total radiation expected, %	89	88	58	27		
High and low 24 hours temperatures, °C	37,14	30.5,15.5	29.5,12	12,7		
Average wind speed at 50 ft, mph	7.9	7.6	11.6	4.2		
Sky cover from sunrise to sunset, %	0	20	70	100		

* –50.7 bar KCl Standard Solution, –50.5 bars measured.
** Data from Hanford Meteorology Station, Battelle-Northwest Laboratory, near sample location.

Results and Discussion

Table 1 shows leaf water potentials of the four above-mentioned woody species at 8:30 a.m. and 1:15 p.m. on September 21, 1967, a typically sunny day. Ambient atmospheric conditions in the afternoon favored increased transpiration, making water potentials lower in the afternoon than in the morning.

Table 2 shows the water potentials of several plants sampled at various dates. No precipitation was recorded during the sampling period from September 21 to September 29, 1967, while precipitation of 0.29 inch was recorded from September 29 to November 13, 1967. (Almost half of the precipitation occurred during the last five days prior to November 13, 1967.) The increases in water potential as the season advanced were probably due to late fall rains and decreasing atmospheric stress brought about by lower temperatures and high relative humidities. Although soil water conditions undoubtedly were involved, the relative importance of these and atmospheric conditions is indicated by data on watercress, a floating plant with roots entirely in water. Water potential of the leaves of this plant increased from –18.5 bars to –11 bars between September 20 and November 13. In essence, these observations are in accord with a study (Hodges, 1967) in which variations of leaf water potential of conifers responded to changes in atmospheric moisture.

We do not know the degree to which readings were affected by sampling at the ambient temperature indicated and then analyzing at 25°C.

Summary

The operating range of the Spanner thermocouple psychrometer was extended to –100 bars so the low moisture potentials of xerophytes could be measured. This range extension was obtained by use of special thermocouple welds and by increasing the time of Peltier cooling. Water potentials of the detached leaves from several native species in the semidesert area of eastern Washington were measured at selected times of the day and season. Observed values of potential were consistent with stresses imposed by the environment. The lowest potential, –94 bars, was measured on leaves of salt grass (*Distichlis stricta*) in September.

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Literature Cited

Boyer, J. S. 1968. Relationship of water potential to growth of leaves. Plant Physiology 43(7): 1056-1062.

Campbell, G. S., J. W. Trull, and W. H. Gardner. 1968. A welding technique for Peltier Thermocouple Psychrometers. Soil Sci. Soc. Am. Proc. 32: 887-889.

Campbell, G. S., W. D. Zallinger, and S. A. Taylor. 1966. Sample changer for thermocouple psychrometric construction and some applications. Agronomy Journal 58: 315-318.

Hodges, J. D. 1967. Patterns of photosynthesis under natural environmental conditions. Ecology 48: 234-242.

Lambert, J. R., and J. V. Schilfgaarde. 1965. A method of determining the water potential of intact plants. Soil Science 100: 1-9.

Rawlins, S. L., W. R. Gardner, and F. N. Dalton. 1968. In situ measurement of soil and plant leaf water potential. Soil Sci. Soc. Am. Proc. 32: 468-470.

Spanner, D. C. 1951. The Peltier effect and its use in the measurement of suction pressure. Jour. of Experimental Botany 2(5): 145-168.

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Northwest Science

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Predator-Prey Relationships between Coyotes and White-tailed Deer

Introduction

A study was made to understand better the importance of coyote predation on white-tailed deer in northeastern Washington. It was directed toward answering these questions: 1) How important are deer to the over-all diet of the coyote? 2) What segment of the population is most often taken? 3) Under what conditions are deer vulnerable to predation?

Study Area

The study area occupies 800 square miles in the northwestern part of Stevens County, Washington (Fig. 1). The western half of the area is drained by the Columbia River, the eastern half by the Colville River. The Huckleberry Mountain Range forms the height of land, and has an average elevation of 4500 ft. Rainfall is light; the 10-year average for 1957-67 was 17.36 in. annually as compiled by the U.S. Weather Bureau in Colville.

The vegetation forms a complex mosaic which varies with respect to slope, elevation, and rainfall. Blue bunch wheatgrass (*Agropyron spicatum*) and bluegrass (*Poa* spp.) occur on dry sites. Ponderosa pine (*Pinus ponderosa*), larch (*Larix occidentalis*), douglas fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*) occur with increasing moisture. Snowberry (*Symphoricarpos albus*), mountainspray (*Holodiscus discolor*), mallow ninebark (*Physocarpus malvaceus*), and huckleberry (*Vaccinium* spp.) are common understory species.

Materials and Methods

Importance of deer in the coyote diet was investigated by analyzing stomach and scat contents. Coyotes were trapped between June and September 1967, and February and June 1968. Contents of 31 stomachs were analyzed, and the volume occupied by each item was estimated. Only 12 coyotes showed items in their stomachs that could be classified as food; the remaining 19 were either empty or contained only bait. Percentage of frequency of occurrence and the aggregate percent volume (Martin *et al.*, 1946) were calculated. During the same period 102 coyote scats were analyzed. Scats were broken apart and the items identified. Hair, teeth, claws, and portions of skulls provided means for identification. Percent frequency of occurrence was calculated. A collection of small mammals was made on the study area which provided means of identifying hair and bones recovered from scats.

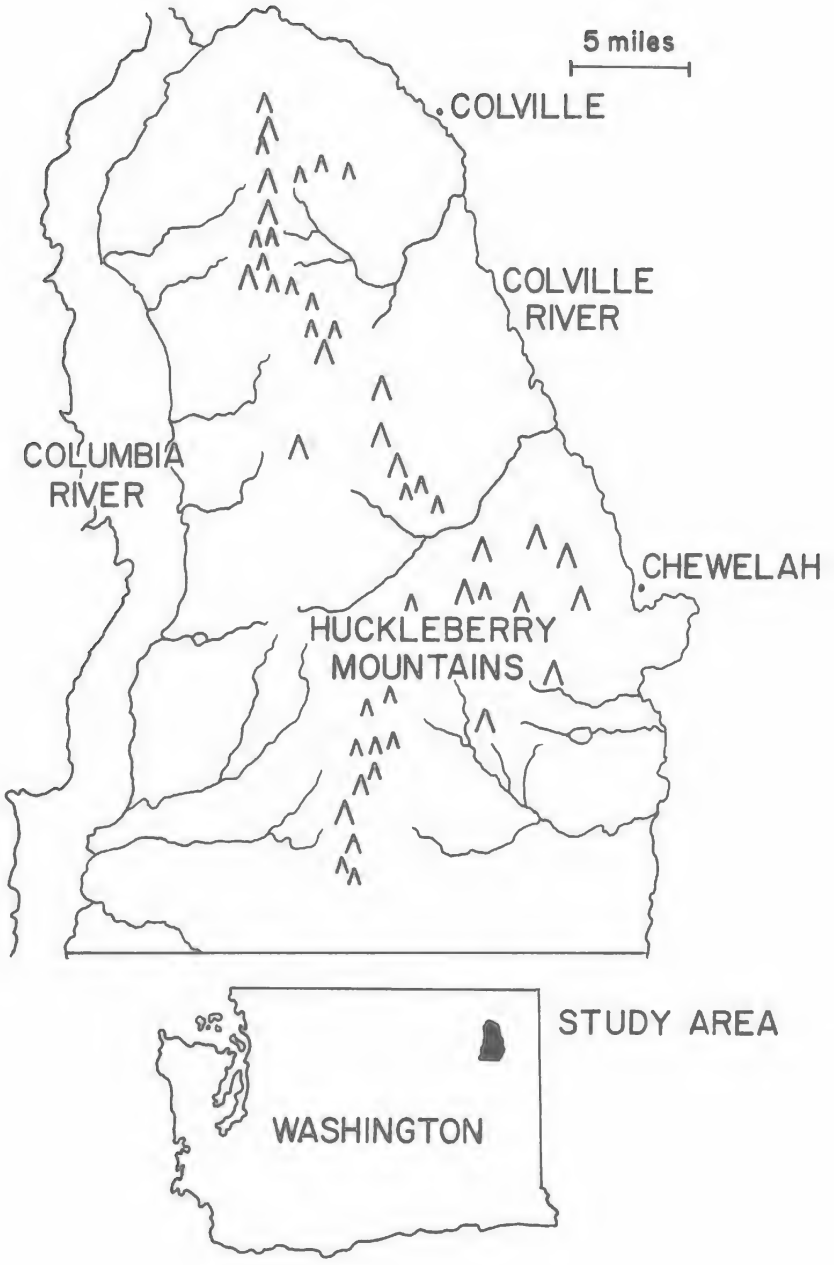

Figure 1. Study area in northeastern Washington.

Lower jaws from 43 deer found dead in the field were collected to study the age-classes most susceptible to mortality. Tooth wear was the sole criterion on which estimated age was based (Severinghaus, 1949). Eleven deer which were known to have died from causes other than predation were used to study feeding patterns of coyotes on carrion. This provided a means to distinguish deer killed by coyotes from those fed upon secondarily. Several coyote feeding characteristics were outstanding in freshly killed deer (dead from one month to less than 24 hrs.) found in the field that were never observed in deer known to have been fed upon as carrion. These characteristics are listed in order of constancy in Table 1. The patches of hide

TABLE 1. Criteria used to distinguish deer killed by coyotes from those fed on as carrion.

1) Large patches of hide leading to the carcass
2) Separation of vertebral column in the thoracolumbar region of adults and at the atlas of fawns
3) Nasal and maxillary bones chewed away
4) Ribs, vertebrae, and scapulae chewed[1]
5) Limbs widely scattered[1]

[1] General characteristics of coyote feeding whether on coyote-killed deer or carrion.

are thought to result from biting and tearing action of attacking coyotes. This criterion is believed to be the most reliable in determining whether or not the animal was killed by coyotes. Observers have reported that deer under attack frequently have large areas of hide torn from the muscles of the belly and rump regions (local residents, pers. comm.; Cahalane, 1947; Cowan, 1947; Pimlott *et al.,* 1969). Patches of hide most often contained long, white hairs which indicate that they came from the rump or belly. Such patches were never found near deer that were known to have died from other causes, even though coyotes were known to have fed secondarily on the carcasses.

Results and Discussion

Importance of Deer to the Coyote Diet

Major sources of prey were rodents and deer; importance of each varied according to seasonal availability. From late winter to spring deer occurred most often in scats, and rodents were second. During this period porcupines and voles (*Microtus* spp.) made up the bulk of rodent occurrences. In late spring and summer rodents and deer reversed their importance in the diet; rodents became the primary food and deer were second (Fig. 2). Analysis of 12 coyote stomachs collected between May and September supports the finding from scat analysis that rodents were the primary food during this period (Table 2) but the sample size is too small to be conclusive. Rodents

TABLE 2. Analyses of food items in coyote stomachs from May to September.[1]

Food Class	Percent Frequency Occurrence	Aggregate Percent Volume
Rodent	66.0	40.6
Deer	41.6	17.4
Insects	25.0	2.4
Plants	8.3	2.2

[1] These data are based on the analyses of 12 stomachs.

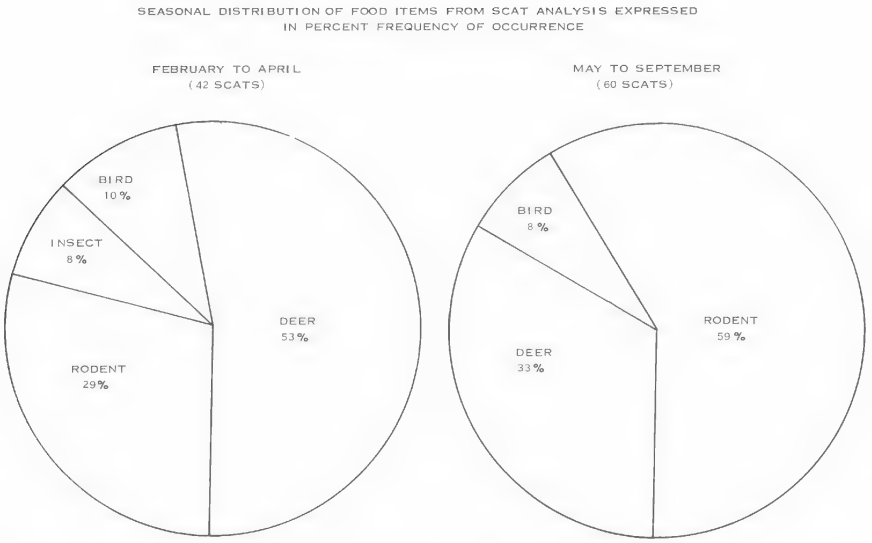

Figure 2. Seasonal distribution of food items from scat analysis expressed in percent frequency of occurrence.

first appeared as the primary food near the end of April when ground squirrels first became available. Fawns comprised 59 percent of the deer remains found in scats and stomachs of coyotes. Almost 80 percent of all rodents eaten were ground squirrels.

By mid-August ground squirrels began to estivate and were unavailable to coyotes. Thus, the availability of food in late August may be a limiting factor to the coyote population since the major summer source of prey becomes unavailable, and fawns are less susceptible to predation and accidents. Such a situation probably exerts a selective pressure against pups since they are more inexperienced and weaker. Emaciated pups in starving condition have been frequently sighted on the study area in early September and help substantiate this conclusion (local residents, pers. comm.).

Predation in Relation to Age of Deer

Age-classes most susceptible to mortality were determined from 43 deer believed to have died from natural causes (*i.e.,* environmental stresses, old age, or predation). These deer were found in the field between February and August. Male deer represented in the collection series had already lost their antlers indicating that they had died sometime after January, more than two months after the close of deer hunting season. This fact and the disparity between the number of mid-age and old-age classes represented suggest that mortality caused by hunting was minimal. Of the 43 carcasses studied, 19 fit the criteria for coyote-killed deer. Others showed characteristics of coyote feeding (Table 1) but probably died from causes other than predation.

Data in Table 3 show that deer under two and over six years of age are most susceptible to mortality factors, including predation. Deer between two and six years of age appear most secure from mortality. Sex ratios in all age-classes were essentially equal. Fawns and yearlings seemed to be most vulnerable to coyotes, perhaps because

TABLE 3. Age distribution of dead deer.

Age	Number of Deer[a]	Percent of Total
Fawn	19 (10)[b]	53.5 (68.5)[c]
Yearling	6 (3)	
2 to 5 years	3 (1)	6.9 (5.3)
6+ years	17 (5)	39.6 (26.2)

[a] Sex ratios were equal in all age-classes.
[b] Numbers in parentheses indicate coyote-killed deer.
[c] Percent of total considered killed by coyotes.

they are inexperienced, weaker, and more dependent upon adults than deer in older age-classes. Almost 69 percent of dead deer considered coyote-kills were fawns or yearlings. Old deer, six-plus years old, comprised almost 40 percent of the dead deer but only 26 percent of coyote-killed deer. That coyotes may pay special attention to fawns is indicated by noting that 53 percent of dead fawns were considered coyote-killed whereas in the six-plus class only 29 percent were coyote-killed. More deer of all age-classes died from natural causes other than predation, suggesting that coyote predation was of a compensatory nature and not limiting to the deer population. The latter conclusion is further supported by the fact that the study area supports a general buck hunting season, a general doe season, and a late buck season.

This pattern of mortality has been described in a number of wild ungulate populations (Murie, 1944; Mech, 1966; Pimlott *et al.,* 1969), and even in the absence of canid predators (Murie, 1940; Pimlott, 1967; Houston, 1968).

Factors Which Contribute to Deer Predation

Most of the dead deer considered coyote kills were found in grassy fields where deer were known to congregate to feed in late winter. In reconstructing the chases it was noted that 65 percent of the dead deer were found on steep hillsides and that patches of hide were almost always uphill from the carcass which suggests a downhill chase. Murie (1940) stated that coyotes may systematically chase deer down slopes and catch them at the bottom. However, Rutter suggested that deer may select the roughest and most difficult terrain in escaping from wolves (Pimlott *et al.,* 1969). That one of these possibilities obtained on the study area is further supported by the following observation. Five coyote-killed deer were found in early spring on Rice Mountain. The mountain has steep slopes and talus slides on the east- and west-facing slopes; the north- and south-facing slopes are gentle with very little exposed rock. All of the dead deer were restricted to the former areas. Thus, it appears that deer are at a distinct disadvantage on steep slopes, and are highly vulnerable to coyotes in such situations. However, the possibility that deer attempt to escape coyotes by choosing rough terrain cannot be ruled out.

Deer in the old-age class may become vulnerable to predation due to a variety of degenerative changes associated with advancing age. This study provided only limited insight into one of these factors. One-third of the old deer exhibited necrotic jaws. Murie (1944) discussed this condition in detail and concluded that it may become a serious handicap to survival.

Acknowledgements

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Literature Cited

Cahalane, V. H. 1947. A deer-coyote episode. J. Mammal. 28: 36-39.
Cowan, I. McT. 1947. The timber wolf in the Rocky Mountain National Parks of Canada. Can. J. Res. 25(1): 139-174.
Houston, D. B. 1968. The Shiras Moose in Jackson Hole, Wyoming. Grand Teton Natural History Association, Tech. Bull. No. 1. 110 pp.
Martin, A. C., R. H. Gansch, and C. P. Brown. 1946. Alternative methods in upland game bird food analysis. J. Wildl. Mgmt. 10(1): 8-12.
Mech, D. L. 1966. The Wolves of Isle Royale. Fauna Series 7. U.S. Government Printing Office, Washington, D.C. 206 pp.
Murie, A. 1940. Ecology of the Coyote in the Yellowstone. Fauna Series 4. U.S. Government Printing Office, Washington, D.C. 206 pp.
————. 1944. The Wolves of Mt. McKinley. Fauna Series 5. U.S. Government Printing Office, Washington, D.C. 238 pp.
Pimlott, D. H. 1967. Wolf predation and ungulate populations. Am. Zool. 7(2): 267-278.
————, J. A. Shannon, and G. B. Kolenosky. 1969. The Ecology of the Timber Wolf in Algonquin Provincial Park. Ont. Dept. Lands and Forests Res. Rep. (Wildlife) No. 87. 92 pp.
Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Mgmt. 13(2): 195-216.

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Errata

Volume 40, no. 3, 91 (1966) *Podabrus marina* Fender should be *Phausis marina* Fender.

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Small Mammal Populations of an Area in Northern Idaho Severely Burned in 1967

Reports of a small rodent population outbreak and consequent extensive damage to vegetation of the Trapper Peak-Sundance Mountain burn (56,000 acres, 1967), Kaniksu National Forest, northern Idaho, prompted this study. Newspaper accounts and inexperienced observers alluded to small mammal densities of 7000-10,000 per acre. Both deer mice (*Peromyscus*) and voles (*Microtus*) were reported to have increased to unusual densities.

Periodic irruptions of vole populations are well documented (Elton 1942), but to our knowledge published accounts do not associate outbreaks with post-burn conditions. Three species of voles occur in northern Idaho; *M. longicaudus* is widespread in distribution, whereas *M. pennsylvanicus* and *M. richardsoni* are more local in occurrence. *M. pennsylvanicus* and *M. longicaudus* are known to irrupt (Krebs *et al.,* 1969; Bailey, 1918). Widespread irruption of vole populations occurred in the Pacific Northwest during the period 1957-58 in cultivated land (Spencer, no date). Assuming a periodicity of four years, a possible population high would occur in 1969-70 in this region.

Deer mice populations are commonly regarded to be very stable (Sadleir, 1965) and noncyclic (Terman, 1968). A possible deviation from these conditions, especially to high densities, is noteworthy from the standpoint of causation and possible social (density) effects (Christian *et al.,* 1965, 1970).

Study objectives were to evaluate the relative abundance and diversity of small mammals on the burn, obtain a measure of the impact of small mammals on the vegetation, and determine if overt signs of social stress were being manifested.

The results reported here did not confirm the presence of unusual densities of small mammals on three areas sampled on the burn in July 1970. However, rodent damage to the shrub stratum had occurred during the previous winter.

Virtually no work has been reported on interactions among fires, small mammals, and succession in the northern Rocky Mountains. Public and private wildland management agencies need quantitative data on these interactions to use in developing management policies following extensive forest and range fires.

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Methods

Three plots, each 100 ft. by 100 ft., were established at or near the center of the long axis of the 56,000 acre burn during July 1970. One plot was approximately 0.5 mile outside the burn and three plots were at low, medium, and high elevations on the west side of Apache Ridge.

Unburned sample plot (1) is covered by a mixed-coniferous forest with a closed canopy and is a *Thuja plicata-Pachistima myrsintes*[2] habitat type (Daubenmire and Daubenmire, 1968). Trees now present are western white pine (*Pinus monticola*), western hemlock (*Tsuga heterophylla*), and western red-cedar (*Thuja plicata*). Thimbleberry (*Rubus parviflorus*) and various ericaceous shrubs are present in the understory. The herbaceous understory is sparse and was not sampled. The slope is 70-80 percent and the aspect is ESE.

Burned sample plot (2), at low elevation, is on a 15-20 percent slope and the aspect is WSW. The habitat type is *Abies grandis-Pachistima myrsinites.* Trees had been selectively cut from the stand prior to the burn. The burned boles of trees in the 40-50 ft. height class remain standing. Grass had been seeded on the plot by accidental drift.

Burned sample plot (3), at mid-slope, is on a 30-40 percent slope and the aspect is WSW. Per-burn stand conditions appeared to have been similar to plot (2). No grass had been seeded on the plot. Plots (2) and (3) were more than a mile from edges of the burn.

Burned sample plot (4), near the ridge top, is on a 40-50 percent slope and the aspect is SSW. The habitat type is *Abies lasiocarpa-Vaccinium scoparium.* Dead standing lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) are present. Grass had been seeded on the plot. The plot is approximately ½ mile from the east edge of the burn.

A small mammal trapping grid was installed on each sample plot. Each grid consisted of 100 traps, 85 museum special and standard snap-traps, and 15 Sherman live-traps (9 in. x 3 in. x 4 in.). One hundred trapping points (10 rows and 10 columns at 10-ft. intervals) were located and marked. Traps were assigned to the "grid" points at random. All traps were baited with peanut butter. Traps remained open for 48 hours and were checked four times at 12-hr. intervals.

Captured animals were killed or removed and sex, reproductive status, weight, total and tail length determined and examined for ectoparasites and gross abnormalities of organ systems. Selected organs (gonads, liver, and stomach) were fixed, sectioned, stained with hematoxylin and eosin and histopathologic studies conducted in search of evidence of tissue abnormalities.

Within plots (2), (3), and (4) the vegetation was sampled at seven "grid" points per plot which were selected at random from the 100 possible points. At each point a circular plot enclosing 12.56 sq. ft. (two-ft. radius) was examined. Flowering stalks, woody stems, and bunches of grass were enumerated for each species present within the circular plot. All stalks and stems which showed evidence of rodent use were enumerated.

[2] Plant names are according to St. Johns, *Flora of Southeastern Washington.*

Results

Small Mammals

The relative numbers and species composition of the mammals trapped on the burn study plots are summarized in Table 1. In addition, one male and female *M. longicaudus* and one male *Zapus princeps* were captured on plot (2). One male *Eutamius amoenus* was captured on plot (4). No animals were trapped on unburned plot (1). Seventeen individuals of four species were trapped on plot (2). Sixteen individuals of two species were trapped on plot (3). Twelve individuals of two species were trapped on plot (4); however, sight records confirmed the presence of *Spermophilus columbianus. Peromyscus maniculatus* was the most commonly trapped animal on the three burn plots. Twenty-three of the 36 *P. maniculatus* were young-of-the-year. No histopathology was detected in gonadal, liver, or stomach tissues of those *P. maniculatus* examined. No abnormal organs were found in the other species examined.

Fleas were the only ectoparasites found on any of the animals examined.

Vegetation Analysis

Results of the vegetation analysis and use appraisal are given in Table 2. Fireweed (*Epilobium angustifolium*) and grasses were the most common plants. Four to seven species of shrubs were present on each plot. By chance, only two shrub species were sampled in plot (3). Unburned plot (1) was not sampled because of time limitations.

Many stems of various shrubs had been peeled during the winter of 1969-70 (Table 2). In the time available it was not possible to obtain a quantitative measure of rodent use of grass and herbs. No grass cuttings were observed.

The amount of bare ground was extremely variable among and within the three plots (Table 2).

Discussion

According to distributional records of Hall and Kelson (1959), 16 species of mammals potentially could have been taken in our trapping in this area. Four species were trapped and two additional species, *Spermophilus columbianus* and *Zapus princeps,* were observed. Apparent absence of shrews is probably, among other factors, correlated with their limited powers of dispersal and the general lack of ground litter on the burn. Microtines with rather specific niche requirements, *e.g., Clethrionomys gapperi, Microtus pennsylvanicus,* and *M. richardsoni* (Hoffmann and Pattie, 1968), probably cannot sustain populations on burns in the northern Rocky Mountains for 5-10 years post-burn, perhaps even longer. In general, few data are available on burns for predicting the time-course relationship between succession and return to equilibrium of small mammal species diversity. Our data indicate species diversity of small mammals is reduced significantly in the years immediately following a burn *i.e.,* from 16 to six species. However, compared to our control plot (1) diversity is increased following a burn. We view this latter result as an artifact of sampling.

Unusually high densities of small mammals on the burn were not substantiated by our trapping procedures. A removal trapping scheme such as we used has a major deficiency in that the actual sample area is unknown. Captures may be used as an index to abundance but not to absolute density. The density of our traps (one per 100 sq. ft.) probably permitted the removal from roughly an acre of most of the resi-

TABLE 1. A summary of the species composition, age, sex, and weights of small mammals captured July 1970 on three 100 x 100 ft. plots within the Trapper Peak-Sundance Mountain burn in northern Idaho.

Species / Age	Sex	Plot No. (2) n	(2) Weight (g) $\bar{x}$±SD	(2) M*	Plot No. (3) n	(3) Weight (g) $\bar{x}$±SD	(3) M	Plot No. (4) n	(4) Weight (g) $\bar{x}$±SD	(4) M
Peromyscus maniculatus										
Adult	Male	1	20	–	5	20.5±1.1	19–22	1	28	–
	Female	2	22.5±2.1	21–24	2	23 ±5.7	19–27	1[a]	31	–
Immature	Male	5	14.3±0.3	13–15	1	14	–	6	13.6±1.5	11.5–15.5
	Female	4	13.3±0.3	12–14	4	13.4±1.6	12–15	3	11.7±2.5	9–14
Penacomys intermedius										
Adult	Male	1**	–	–	2	35.5±0.2	35–36	–	–	–
	Female	–	–	–	1††	34.5	–	–	–	–
Immature	Female	–	–	–	1	10.5	–	–	–	–
TOTAL CAPTURES		13			16			11		

* Maximum and minimum values.
** Not weighed but less than 25 g.
*† 1 *P. maniculatus* not sexed or weighed.
[a] Pregnant, 5 embryos.
†† Pregnant, 6 embryos.

TABLE 2. Densities of plant species (mean ($\bar{x}$), standard deviation (Sd), and maximum and minimum values (m) and rodent use (no. of stems used) on three sample plots located within the Trapper Peak-Sundance Mountain burn, northern Idaho, July 1970. Each sample value is a mean derived from seven circular plots enclosing 12.56 sq. ft. (2 ft. radius) selected at random within the sample plots.

	Plots											
	(2)				(3)				(4)			
Plant Species	$\bar{x}$	Sd	m	Use	$\bar{x}$	Sd	m	Use	$\bar{x}$	Sd	m	Use
Rubus sp.	3.9	6.6	0–18	12	–	–	–	–	–	–	–	–
Grass	13.9	7.4	3–21	0	1.7	2.8	0–7	0	20.0*	–	5–60	0
Epilobium angustifolium	10.4	10.6	1–32	0	28.3	18.7	11–55	0	21.1	15.1	5–50	0
Sphaeralcea rivularis	1.1	1.9	0–5	0	–	–	–	–	–	–	–	–
Pachistima myrsinites	0.7	1.1	0–3	0	–	–	–	–	1.4	2.2	0–6	16
Rubus parviflorus	0.7	1.1	0–3	1	–	–	–	–	7.3	7.3	0–17	0
Equisetum sp.	0.14	–	0–1	0	–	–	–	–	–	–	–	–
Aretostaphylos Uva-ursi	0.14	–	0–1	0	0.43	1.2	0–3	0	2.4	4.8	0–13	39
Trilium sp.	0.29	0.24	0–2	0	–	–	–	–	–	–	–	–
Ceanothus sanguineus	0.14	–	0–1	1	–	–	–	–	–	–	–	–
Vaccinium membranaceum	0.43	1.2	0–3	2	–	–	–	–	–	–	–	–
Herb, unknown	–	–	–	–	3.1	7.5	0–20	0	–	–	–	–
Ribes viscosissimum	–	–	–	–	1.1	2.3	0–6	6	–	–	–	–
Salix sp.	–	–	–	–	–	–	–	–	4.6	4.2	0–12	6
Spiraea betulifolia	–	–	–	–	–	–	–	–	7.9	7.0	0–20	6
Symphoricarpos albus	–	–	–	–	–	–	–	–	5.6	11.3	0–30	5
Rosa sp.	–	–	–	–	–	–	–	–	0.4	1.3	0–3	1
% Bare Ground	32	21	8–60		74	15	50–95		5% or less throughout			

* Mean for grass on plot (4) given as percent coverage.

dent *P. maniculatus* capable of entering traps. The actual area sampled for microtines was perhaps ½ acre. Complete removal of all residents does not seem likely (Wiegert and Mayenschen, 1966). Since numerous set traps were always available throughout our sampling, we conclude that high densities of *Peromyscus* and high numbers of associated species did not occur on the burn plots.

Results of trapping small mammals in other areas support our conclusion that unusual densities did not occur on the burn. Catlett and Brown (1961) in mid-summer on an unburned area in Colorado on a 100 x 100 ft. plot in 143 trap nights captured 69 individuals of six species, including 49 *Peromyscus maniculatus.* Gashwiler (1959) estimated 6.2 *P. maniculatus* per acre one month post-burn (slash burn) in Oregon. Our unburned plot (1) yielded no animal captures. Previous work by Hoffman (1960) in climax coniferous stands in the northern Rocky Mountains indicated extremely low populations, *i.e.,* three to five *P. maniculatus* in 405 "snap-trap days." Likewise, Gashwiler (1959) reported from 0.0 to 2.5 *P. maniculatus* per acre in old growth douglas fir (*Pseudotsuga menziesii*). Comparative data on all of the species encountered by us are not available.

According to the theory of small mammal population regulation advocated by Christian *et al.* (1965, 1968, and 1970), declining birth rates or declining survival rates are symptomatic of populations reacting to over-population. Examination of our trapping data (Table 1) suggests normal reproduction was occurring in the populations. We do not believe any depressant density-dependent processes were operating at the time of sampling.

A major result of a burn appears to be a marked change in the species importance in energy flow through small mammals. Microtines, shrews, and various sciurids are dominant in these energy transfers among unburned habitats in the northern Rocky Mountains. Following a burn, granivores are favored (Tevis, 1956; Cook, 1959; Gashwiler, 1959; Lawrence, 1966) in the initial stages of secondary succession. Cook (1959) reported an irruption of *Reithrodontomys* during a period of maximum seed production. Both Cook (1959) and Lawrence (1966) have documented the shift in *Peromyscus* species abundance to favor *P. maniculatus* in the years following burns. *P. maniculatus* is particularly suited to exploit burns since it shows a preference in its diet for seeds of grasses and herbs and insects (Jameson, 1952; Drickamer, 1970). Also, often no other small mammal with similar feeding habits is present to compete.

The rodent feeding which we documented (Table 2) was almost exclusively bark peeling of shrubs species. Previous work (authors, unpublished data at WSU) strongly suggested this feeding was done by *M. longicaudus.* We do not know if *P. intermedius* is a stem peeler. The shrub species utilized by the rodents are also important sources of browse for wild ungulates.

Much of the Trapper Peak-Sundance Mountain burn was seeded to grass (several species) to aid in soil erosion control (William O'Brien, personal communications). In addition, reforestation efforts included aerial seeding and hand planting of selected conifers. Published accounts previously cited have shown that even with natural seeding, burned areas soon support normal to somewhat higher populations of granivores, *e.g., P. maniculatus.* A large-scale successful seeding operation can only accelerate the repopulation of a burn by *Peromyscus.* At present there is no *a priori* way of predicting population response of other small mammals. Documentation of population biology

of microtines in years following burns seems particularly important. These species are capable of extensive barking of planted trees (Black *et al.,* 1969) and of unpredictable population growth. Optimization of the timing of seeding grass for erosion control and of reforestation efforts on burned areas clearly should take into account the impact of small mammals (Hooven, 1958). The interactions of fire, succession, and small mammal communities are at present unexploited by critical research.

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Literature Cited

Bailey, V. 1918. Wild Animals of Glacier National Park. The Mammals. Nat. Park Ser., Washington, D.C. 102 pp.

Black, H. C., E. J. Dimmock II, W. E. Dodge, and W. H. Lawrence. 1969. Survey of animal damage on forest plantations in Oregon and Washington. Trans. 34th N. Am. Wildl. Nat. Resources Conf. Pp. 388-408.

Catlett, R. H., and R. Z. Brown. 1961. Unusual abundance of *Peromyscus* at Gothic, Colorado. J. Mamm. 42(3): 415.

Christian, J. J. 1968. Endocrine-behavioral negative feed-back responses to increased population density. Ed. Cent. Natl. Rech. Sci. (Paris) m 173: 289-322.

————. 1970. Social subordination, population density, and mammalian evolution. Sci. 168(3927): 84-90.

————, J. A. Lloyd, and D. E. Davis. 1965. The role of endocrines in the self-regulation of mammalian populations. Pp. 501-578. *In* G. Pincus ed., Recent Progress in Hormone Research. Academic Press, New York.

Cook, S. F., Jr. 1959. The effects of fire on a population of small rodents. Ecol. 40(1): 102-108.

Daubenmire, R., and Jean B. Daubenmire. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Technical Bull. 60, Washington Agric. Exper. Station. 104 pp.

Drickamer, L. C. 1970. Seed preferences in wild caught *Peromyscus maniculatus bairdii* and *Peromyscus leucopus noveboracensis*. J. Mamm. 51(1): 191-194.

Elton, C. 1942. Voles, Mice, and Lemmings. Oxford: Clarendon Press. 496 pp.

Gashwiler, J. S. 1959. Small mammal study in west-central Oregon. J. Mamm. 40(1): 128-139.

Hall, E. R., and K. R. Kelson. 1959. The Mammals of North America. The Ronald Press Company, New York. 1083 pp. 2 Vols.

Hoffman, G. R. 1960. The small mammal components of six climax plant associations in eastern Washington and northern Idaho. Ecol. 41(3): 571-572.

Hoffmann, R. S., and D. L. Pattie. 1968. A Guide to Montana Mammals: Identification, Habitat, Distribution and Abundance. University of Montana, Missoula. 133 pp.

Hooven, E. 1958. Deer Mouse and Reforestation in the Tillamook Burn. Research Note No. 37, Oregon Forest Lands Res. Cent. 31 pp.

Jameson, E. W., Jr. 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boylei,* in the northern Sierra Nevada, California. J. Mamm. 33(1): 50-60.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: Demographic changes in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecol. 50(4): 587-607.

Lawrence, G. E. 1966. Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. Ecol. 47(2): 278-291.

Sadleir, R. M. F. S. 1965. The relationship between agonistic behavior and population changes in the deermouse, *Peromyscus maniculatus* (Wagner). J. Anim. Ecol. 34(2): 331-352.

Spencer, D. A. No date. Biological and control aspects. Pp. 15-25. *In* The Oregon Meadow Mouse Irruption of 1957-1958. Fed. Coop. Exten. Ser., Oregon State College.

Terman, C. R. 1968. Population dynamics. Pp. 412-450. *In* J. A. King ed. Biology of *Peromyscus* (Rodentia). Spec. Publ. No. 2, Amer. Soc. of Mammalogists.

Tevis, L., Jr. 1956. Effect of slash burn on forest mice. J. Wildl. Mgmt. 20(4): 405-409.
Wiegert, R. G., and J. C. Mayenschein. 1966. Distribution and trap response of a small wild population of cotton rats (*Sigmodon h. hispidus*). J. Mamm. 47(1): 118-120.

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Aberrant Coloration in Microtus pennsylvanicus from Grand Teton National Park

An aberrant (piebald spotted) adult male *Microtus pennsylvanicus pullatus* (Fig. 1) was captured while conducting an ecological investigation of small mammals in Grand Teton National Park. The pelage was normal except for the large white dorsal spots. The vole's testes were scrotal and its seminal vesicles were enlarged. This was the only

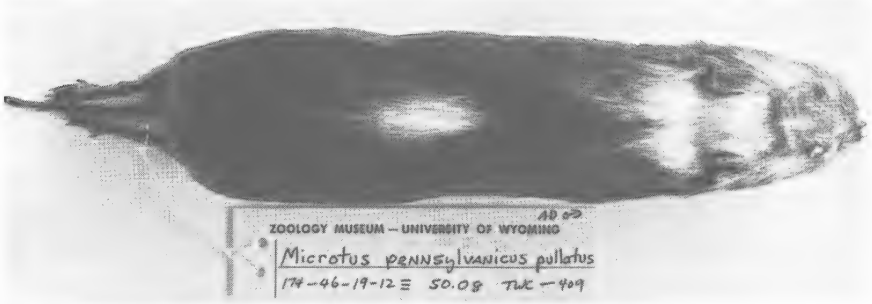

Figure 1. Piebald spotted adult male *Microtus pennsylvanicus pullatus* captured in Grant Teton National Park, Wyoming.

individual showing aberrant coloration out of over 300 meadow voles captured (approximately 14,000 trap-nights in summers of 1968 and 1969), thus suggesting that this type of aberrant coloration may be an unusual occurrence in natural environments.

Coat color varieties in this species have been described by Snyder (1930) and Clark (1938), and Owen and Shackelford (1942) have discussed probable homologies. Aberrant colorations in *M. pennsylvanicus* show a striking similarity to those described by Frank and Zimmermann (1957) in *M. arvalis,* demonstrating Vavilov's (1922) law of homologous variation. Many spotting mutants may have pleiotropic effects. White-spotting, anemia, and homozygous lethality are pleiotropic effects of dominant mutations in *M. arvalis* (Searle, 1968).

The apparent rarity of such aberrant-colored individuals may be accounted for by a combination of three factors: 1) the mortality among microtine rodents is usually very high, 2) a piebald spotted vole may be easily visible and thus more vulnerable to predation, and 3) in a homozygous condition, this type of aberrant coloration may be lethal.

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Literature Cited

Clark, F. H. 1938. Inheritance and linkage relations of mutant characters in the deer mouse, *Peromyscus maniculatus*. Contrib. Lab. Vert. Genetics, Univ. Mich. 7: 1-11.

Frank, F., and K. Zimmermann. 1957. Färbungs-mutationen der feldmaus. Z. Saugetierk. 22: 87-100.

Owen, R. D., and R. M. S. Shackelford. 1942. Color aberrations in *Microtus* and *Pitymys*. J. Mammal. 23: 306-314.

Searle, A. G. 1968. Comparative Genetics of Coat Colour in Mammals. Logos Press (London). 308 p.

Snyder, L. L. 1930. Color mutants in *Microtus*. J. Mammal. 11: 83.

Vavilow, N. I. 1922. The law of homologous series in variation. J. Genet. 12: 47-89.

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Ecology of the Western Jumping Mouse in Grand Teton National Park, Wyoming

Jumping mice are widely distributed over northern North America (Hall and Kelson, 1959). The eastern jumping mice (*Z. hudsonius* and *Napaeozapus insignis*) have been the subject of numerous studies (Bower and Cade, 1966; Quimby, 1951; Sheldon, 1934; Whitaker, 1963). The western jumping mouse (*Z. princeps*), however, has not been extensively investigated. Most studies on this species are limited to ecological notes and taxonomy (Davis, 1939; Krutzch, 1954; Negus and Findley, 1959; Long, 1965) except for recent studies by Brown (1967 and 1970).

The purpose of this study was to elucidate the ecology, *i.e.,* activity patterns, habitat affinities, reproduction, and food uses of the western jumping mouse in Grand Teton National Park, Wyoming.

Study Area

This study was conducted in the northern part of Jackson Hole, Wyoming in Grand Teton National Park. This area has been described by Reed (1952) and Craighead and Craighead (1952). The elevation of the region is about 6750 ft. The geology of the Teton landscape has been described by Love and Reed (1968).

The climate is characterized by long cold winters, deep snows, a short growing season, and low mean annual temperatures. During the study period (May through August) the average temperature is about 51° F. Mean annual temperature is 34.3° F. Frost-free period averages approximately 60 days. Snowfall has been recorded every month of the year and averages 136.9 in. Mean annual precipitation is about 21.5 in. Dice (1943) classified the area into the "Montanian Biotic Province" and this same area falls within Cary's "Transitional Life Zone" (1917).

Methods of Investigation

Habitat affinities were ascertained by trapping six different plant communities. A scheme of habitat analysis, adapted from Whitaker (1963), was used to measure the following parameters: 1) plant cover, 2) soil moisture, and 3) distance to water. The type of trap (snap or Sherman) and number and sex of the mammals captured were recorded. Traps were set at each location and left for three to six days, after which they were moved to a new site. Snap traps were baited with peanut butter and oatmeal and live traps with oatmeal and sorghum. The study extended from June to August 1968 and from May to August 1969. A total of 166 western jumping mice were captured. The six plant communities sampled for *Zapus* are briefly described below and are, in part, after Reed (1952):

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1. *Sedge Meadow Community.* This community is underlain by a very firm sod and is often covered for prolonged periods during parts of the year by standing water to a depth of a few centimeters. Sedges (*Carex* spp.) grasses (mostly *Aleopecurus aequalis* and *Hordeum brachyantherum*) and forbs (*Dodecatheon pauciflorum* and *Gentiana thermalis*) are abundant along with several species of the genus *Equisetum.* The sedge meadow community is superseded by the sedge-grass meadow community in the successional sequence of the area.

2. *Sedge-Grass Meadow Community.* This community is found where slightly elevated areas are present. Several different species of *Carex* are present and dominant grasses include *Agropyron trachycaulum, Agrostis hiemalis, Bromus inermis,* and *Poa palustris.* Approximately 30 species of forbs occur, prominent among which are the clovers (*Trifolium* spp.). This community is extremely productive of a good variety and yield of forage.

3. *Shrub-Swamp Community.* This community is found on sites where the water table is very near the surface and where previous vegetation has produced a considerable degree of stability. Each stand is an irregular aggregation of shrubs, mostly willows (*Salix* spp.). A vigorous growth of forbs and grasses occurs in the reduced light intensity and the abundant moisture under the canopy formed by the shrubs. Conspicuous and common grasses include *Bromus* spp., *Calamagrostis* spp., and *Poa* spp. Among the characteristic and most conspicuous forbs are *Aconitum columbianum, Aster intergrifolius, Castelleja* spp., and *Ranunculus* spp.

4. *Shrub-Sedge-Grass-Savanna Community.* In some places, instead of occurring in disjunct stands, the willows occur in irregular aggregations interspersed with various sedges, grasses, and forbs. The species present in this community are a combination of plants found in the three communities listed above.

5. *Aspen Community.* On the more level sites adjacent to meadows or swamps are aspen groves characterized by closed canopies, dense shade, and forbs and grasses. Although the soil is never so completely saturated as in certain adjacent shrub-swamps, very moist conditions prevail early in the growing season, and diminish during the summer and early fall. Seventy-eight plant species have been found in aspen groves on the moist flats.

Populus tremuloides dominated this community. Forbs included *Aster intergrifolius, Helianthella quinquenervis, Lupinus parviflorus, Osmorhiza* spp., *Angelica pinnata, Delphinium occidentale, Epilobium angustifolium, Hackelia* spp., and *Rudbeckia occidentalis.*

6. *Big Sagebrush Community.* The most widespread and conspicuous of the plant communities of the entire Jackson Hole region is the sagebrush community. Floristically this community is characterized by a rich assemblage of growth forms. Several species of shrubs occur as integral components of the community. Big sagebrush (*Artemisia tridentata*) is clearly the controlling dominant in almost all instances. Only antelope brush (*Purshia tridentata*) and threetip sagebrush (*Artemisia tripartita*) exert anything approaching codominance with big sagebrush in a few localized areas.

The grasses are represented by some 20 or more species which contribute significantly to the ground cover beneath the shrubs. The wheat grasses (*Agropyron* spp.), bromegrass (*Bromus* spp.), fescue (*Festuca idahoensis*), june grass (*Koleria cristata*), blue grass (*Poa* spp.), and needle grass (*Stipa* spp.) are especially abundant and important in this community. Over 100 species of forbs are found in the big sagebrush community, conspicuous and abundant among which are various species of *Antennaria, Arenaria, Aster, Erigeron, Eriogonum, Lomatium, Potentilla,* and *Senecio.*

Plant cover values were determined as follows: *Fair*—ground incompletely covered by vegetation or vegetation not too dense. A mouse could find hiding places but would not be able to move freely about without being seen from above. *Good*—ground covered by dense vegetation. A mouse would not be visible from above. *Very Good*—cover very dense and usually at least waist high. A mouse would be invisible from above.

Soil moisture at each trapping location was determined as follows: *Wet*—usually standing water but generally less than 10 cm deep. *Moderate*—soil damp or spongy underfoot, no standing water. *Dry*—soil dry or nearly so. Good agricultural land. Distance to the nearest standing water was measured in meters.

All animals collected were examined as to stomach contents. Stomach contents were first washed and then separated with the aid of a microscope and all identifiable material was noted. A plant histological collection of some common plants of the study area was used to identify stomach contents. Stomach contents were first identified on a qualitative basis; then a volumetric estimate was made to the nearest 5 percent for each item. The mean volumetric estimates and the frequencies of occurrence of each

food item were calculated. Chi square tests were used to confirm whether *Zapus* was dependently distributed in relation to parameters of habitat.

Results and Discussion

Seasonal Activity Patterns

In 1969, trapping began on 23 May, and the first western jumping mouse was captured the following night. The first female was caught five days later on 29 May. From 24-31 May, 20 western jumping mice were collected; 18 of these were males. In early June (1-15) male mice were caught about twice as frequently as were females (21 males to 13 females). By late June (16-30) sex ratios were nearly equal (38 males to 41 females). Females comprised the larger portion of captured mice throughout July. During the first half of the month (July 1-15), 14 females and 10 males were collected, whereas only three males and six females were trapped during the last part of the month. No trapping effort was made in early August (1-15) of either year. Trapping after the 15th of August, however, yielded no western jumping mice.

From trapping results estimates can be made of the amount of time western jumping mice were active above ground. Adult males were active from mid-May until late July or early August, a period of about 75 days. Adult females were active for about the same length of time; they emerged from hibernation, however, a week or so later than males in the spring and entered hibernation probably a week or so later than males in late summer. As a population, western jumping mice were active above ground from mid-May to early August (about 2½ to 3 months) during the two years of study.

Brown (1967) found that the western jumping mouse was active for about 3½ to 4 months at 8500 ft., 3-3½ months at 9500 ft., and 2½ months at 10,500 ft. in the Medicine Bow Range of southern Wyoming. My study area (6750 ft.) lies about 190 miles north and about 200 miles west of the Medicine Bow Range. Western jumping mice in the Jackson Hole area were active above ground about 2-2½ months, similar to the population of western jumping mice at 10,500 ft. in Brown's (1967) study. Brown (1967) in the western jumping mouse and Whitaker (1963) and Quimby (1951) in the meadow jumping mouse (*Zapus hudsonius*) in New York and Minnesota, respectively, reported that in the spring males appeared active above ground about 15 days before females. The present study varies somewhat from these figures. Intensive trapping beginning earlier in the year in the Jackson Hole area would provide more precise dates of annual arousal from hibernation.

Other than Brown's studies (1967 and 1970), little has been published concerning hibernation of *Z. princeps*. Data presented by Grinnell, Dixon, and Linsdale (1930), Davis (1939), and Bailey (1932) suggested that, starting in July, fat deposits begin to be laid down and by August or early September, animals are excessively fat. The start of hibernation is dependent then upon the arrival of a heavy cold snap (Krutzsch, 1954).

Habitat

According to Davis (1939) the present distribution of the genus *Zapus* suggests that it has been present in the Great Basin area at least since the Pleistocene. It has then had sufficient time to spread to all suitable habitats.

Zapus princeps occurs most commonly adjacent to streams in alder, aspen, or stands of willow, where the moist ground supports a heavy undergrowth of herbs (Borell and Ellis, 1934; Davis, 1939; Kellogg, 1916; Linsdale, 1938; Svihla, 1931). Within these habitat types western jumping mice numbers seem to vary considerably from year to year as well as seasonally (Krutsch, 1954).

The Chi-square test, assuming the "Null Hypothesis," was employed to analyze success between live and snap traps (Table 1). The resulting Chi-square value was

TABLE 1. Chi-square test, assuming the "Null Hypothesis," applied to live and snap trap results in capturing *Zapus princeps utahensis* in Grand Teton National Park, Wyoming.

Trap-Nights		O	E	O-E	D^2	$\frac{(O-E)^2}{E}$
Live	3253	53	27	−26	676	25.04
Snap	6683	28	54	+26	676	12.52
	9936	81	81			$X^2=37.56$

highly significant. As a result, live and snap traps results are considered separately.

Table 2 gives the relationship of live-trapped *Zapus* to plant communities, plant cover, soil moisture, and distance to water. Table 3 presents the same relationships for snap-trapped western jumping mice. The Lowland Aspen community showed

TABLE 2. Relationship of live trapped western jumping mice (*Zapus princeps utahensis*) to plant communities, plant cover, soil moisture, and distance to water in Grand Teton National Park.

Environmental Feature	Trap-Nights	*Zapus*	*Zapus* per 100 Trap-Nights
Plant Community (Chi-Square=48.2, 5 df)			
Sedge-Meadow	590	0	0.0
Sedge-Grass	225	0	0.0
Shrub-Swamp	660	6	0.9
Shrub-Sedge-Grass-Savanna	557	17	3.0
Lowland Aspen	743	28	3.7
Big Sage Brush	478	2	0.4
	3253	53	
Plant Cover (Chi-Square=38.2, 2 df)			
Very good	1230	34	2.8
Good	938	11	1.1
Fair	1316	0	0.0
	3484	45	
Soil Moisture (Chi-Square=17.2, 2 df)			
Wet	628	0	0.0
Moderate	1784	38	2.1
Dry	798	7	0.8
	3210	45	
Distance to Water (Chi-Square=65.2, 3 df)			
0-25 m	643	10	1.5
26-50 m	909	26	2.8
51-50 m	1264	0	0.0
101-200 + m	944	0	0.0
	3760	36	

TABLE 3. Relationship of snap trapped western jumping mice (*Zapus princeps utahensis*) to plant communities, plant cover, soil moisture, and distance to water in Grand Teton National Park.

Environmental Feature	Trap-Nights	*Zapus*	*Zapus* per 100 Trap-Nights
Plant Community (Chi-Square=92.5, 5 df)			
Sedge-Meadow	1114	0	0.0
Sedge-Grass	1370	0	0.0
Shrub-Swamp	720	4	0.5
Shrub-Sedge-Grass-Savanna	1096	0	0.0
Lowland Aspen	1228	24	2.1
Big Sage Brush	1155	0	0.0
	6683	28	
Plant Cover (Chi-Square=68.1, 2 df)			
Very Good	2187	35	1.6
Good	2508	0	0.0
Fair	1757	1	0.0
	6425	36	
Soil Moisture (Chi-Square=8.7, 2 df)			
Wet	390	0	0.0
Moderate	4936	36	0.7
Dry	1400	2	0.1
	6726	38	
Distance to Water (Chi-Square=22.0, 3 df)			
0-25 m	2206	28	1.2
26-50 m	866	7	0.8
51-100 m	1395	10	0.7
101-200 + m	1709	0	0.0
	6176	45	

the highest Capture Index (CI) for both live traps (CI = 3.7) and snap traps (CI = 2.1). Live traps in the Shrub-Sedge-Grass-Savanna community produced a CI (3.0) nearly as large as in the Lowland Aspen community. Mice were also live-captured in the Shrub-Swamp community (CI = 0.9) and Big Sage Brush community (CI = 0.4). The two mice captured in the Big Sage Brush community probably represent transient animals and not members of a resident population. Snap traps captured no *Zapus* in any community other than the Lowland Aspen.

The Very Good class of plant cover yielded the largest number of mice per trap effort for both live (CI = 2.8) and snap traps (CI = 1.6). Again live traps showed a greater CI than did snap traps. A few mice were live captured in the Good class of plant cover (CI = 1.1). No *Zapus* were taken with live traps in the Fair class or with snap traps in the Good class.

Western jumping mice occupied, almost solely, in situations showing moderate soil moisture conditions. Both live (CI = 2.1) and snap (CI = 0.7) traps results were similar in demonstrating this distribution. In Dry situations, however, live traps showed a CI of 0.8 whereas snap traps had a CI of 0.1.

Most western jumping mice were captured within 50 m of standing water; many mice were live trapped (CI = 1.5) nearer standing water (0-25 m). Snap-trapping results showed a somewhat different distribution of jumping mice relative to standing water. The greatest CI from snap trapping was 1.2 (0-25 m from standing water), next highest CI was 0.8 (26-50 m), and a few mice (CI = 0.7) were snap-

trapped even further from standing water (51-100 m). No *Zapus* were captured further than 100 m from standing water with either live or snap traps.

Reproduction

Seasonal changes in mean testicular and mean seminal vesicle lengths for adult western jumping mice are given in Figure 1. The peak in mean testicular length (7.70 mm, N=11) was reached about two to three weeks (June 1-15) after *Zapus* were first captured in late May. During late May mean length was 7.44 mm (N=18). However, peak seminal vesicle length (8.05 mm, N=18) was reached in late May (24-31) when western jumping mice were first captured. Seminal vesicle length was taken as an index of androgen secretion by interstitial cells. Thus seminal vesicles reached maximum length a couple of weeks before testes (Fig. 1). Mean testes lengths steadily decreased (June 16-30, 6.58 mm, N=38; July 1-15, 5.88 mm, N=9) to a low in midsummer (July 16-30, 4.33 mm, N=3) just before hibernation. Mean seminal vesicles followed a similar pattern of seasonal regression (June 1-15, 6.82 mm, N=11; June 16-30, 6.26 mm, N=38; July 1-15, 5.55 mm, N=9; July 16-31, 4.00 mm, N=3).

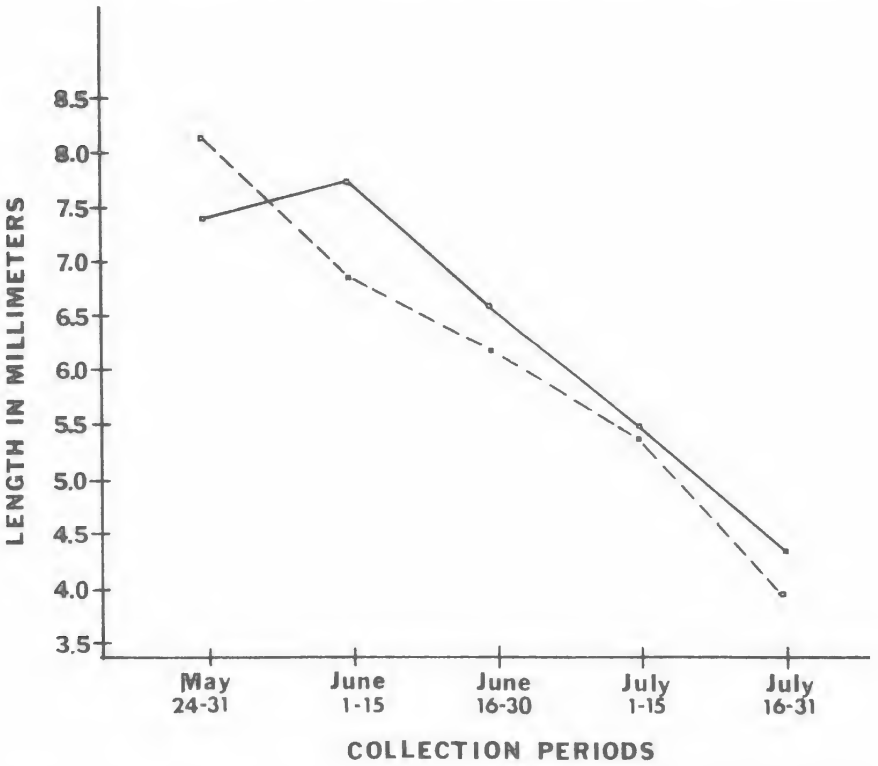

Figure 1. Seasonal changes in mean testicular (solid line) and mean seminal vesicle length (dashes) for adult western jumping mice (*Zapus princeps utahensis*) from Grand Teton National Park, Wyoming.

Brown (1967) has documented histological changes of the testes accompanying the seasonal changes in lengths and weights.

Figure 2 gives the seasonal changes in mean testicular and mean seminal vesicle weights for adult western jumping mice. Mean testicular and seminal weights followed a pattern similar to that of seminal vesicle and testicular lengths, respectively. Mean testes weight, from a peak in late May (99 mg, N=18), fell throughout the summer (June 1-15, 91 mg, N=11; June 16-30, 68 mg, N=28; July 1-15, 59 mg, N=9; July 16-31, 44 mg, N=3). Mean seminal vesicle weights peaked in early June (1-15) (98 mg, N=11) about three weeks after mice were first captured in late May when they weighed 93 mg (N=18). From the high mean weight, seminal vesicles dropped (June 16-30, 53 mg, N=28; July 1-15, 47 mg, N=9) until they reached their lowest mean weight (12 mg, N=3) in late July. Brown (1967) found that the peak seminal vesicle length lagged about two weeks behind weight peaks. He also noted that development and regression of the epididymis in males occurred at roughly the same rate as did testicular changes.

Deterioration of spermatozonia in lumina of the epididymis was apparent in most males three to four weeks following the peak testicular weights (Brown, 1967).

Reproductive condition of 75 adult female western jumping mice captured in 1968

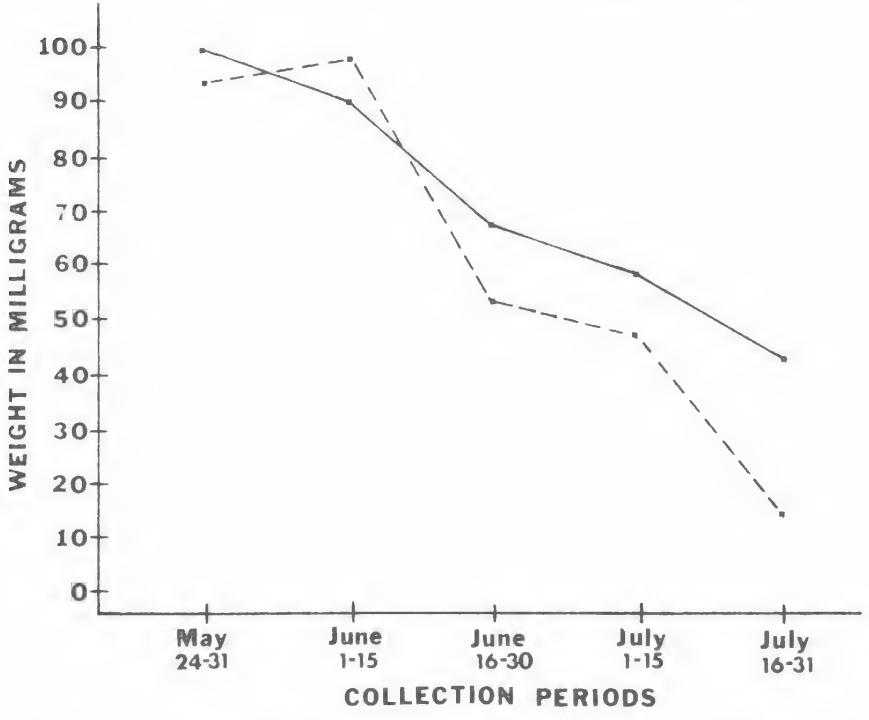

Figure 2. Seasonal changes in mean testicular (solid line) and mean seminal vesicle weight (dashes) for adult western jumping mice (*Zapus princeps utahensis*) from Grand Teton National Park, Wyoming.

and 1969 is given in Table 4. The first pregnant mouse was captured on 14 June and the next on 16 June. Brown (1967) found that adult female *Zapus* come into estrus and breed a few days to one week after they emerge from hibernation. This coincided with the first appearance of large numbers of sperm in the epididymides of males. Placental scars were first encountered in a female captured on 16 June. The gestation has been established by Brown (1967) as 18 days, and on this basis, the latest date this female could have bred was 30 May. Some females were found to be lactating through late July. Brown (1967) suggests that the long lactation period in females compensates for the short gestation period.

TABLE 4. Reproductive condition of 75 adult female western jumping mice (*Zapus princeps utahensis*) collected during two annual above-ground activity cycles (May-August, 1968 and 1969) in Grand Teton National Park, Wyoming.

Condition	May 24-31	June 1-15	June 16-30	July 1-15	July 16-31	Totals
No. pregnant	0	1	15	0	0	16
No. of embryos	0	5	78	0	0	83
Mean no. of embryos	0	5.0	5.2	0	0	5.1
Range in no. embryos	0	5	3-7	0	0	3-7
No. with placental scars	0	0	10	9	5	24
No. of scars	0	0	45	43	25	113
Mean no. of scars	0	0	4.5	4.7	5.0	4.7
Range in no. scars	0	0	3-7	3-6	3-7	3-7
No. without embryos or placental scars	2	12	14	6	1	35
Lactating	0	0	21	9	5	35
No. of animals examined	2	13	39	15	6	75

The mean number of embryos was 5.1 (range 3-7) based on 16 pregnant females. Placental scars average slightly lower (4.7, range 3-7) based on 24 females. One litter per adult female was produced each year of the study. A two and one-half month annual activity cycle precludes the possibility of more than one litter annually. A large number (N=33) adult females did not breed in either year. Only 55 percent (N=40) of all females captured showed signs of having bred. Brown (1970) speculates on the selective pressures acting on *Zapus* to produce one litter annually.

Food Uses

Analyses of stomach contents of 114 *Zapus princeps* are given in Table 5. On a seasonal basis, 82 percent by volume of all stomach contents were seed fragments. Green plant materials composed 18 percent by volume; these were found in 49 percent of all stomachs examined. Arthropods made up only a small fraction of the total diet but were eaten by 62 percent of all mice. Insect consumption was probably incidental to green plant utilization. The only insect identified was a single Collembola.

Two samples were taken from each stomach containing green plant parts and classified into Monocotyledoneae or Dicotyledoneae. Approximately 80 percent of the samples were Monocots and 20 percent were Dicots. Moore (1928) found only "white-starchy, glutinous paste and traces of a brown seed coat" in seven jumping mice collected in early September from central Utah. Bailey (1932), from examination of stomachs collected in New Mexico, remarked "that the food of this mouse was almost entirely seeds of grass and grasslike plants and that the stomach contents almost always were perfectly clean white dough from shelled kernels of small seeds."

TABLE 5. Summary of analyses of stomach contents of 114 western jumping mice. Top figures are mean volumetric estimates calculated to the nearest 1 percent; figures in parentheses are percent frequencies of occurrence; T indicates trace only (less 1 percent).

Stomach Contents	Collection Periods				
	May (24-31) (N=18)	June (1-15) (N=37)	June (16-30) (N=46)	July (1-15) (N=13)	Mean
Green Plant Materials	13 (23)	20 (82)	31 (67)	10 (25)	18 (49)
Seed Fragments	85 (100)	80 (100)	76 (100)	90 (100)	82 (100)
Arthropods	T (20)	T (70)	T (80)	T (80)	T (62)
Parasitic Roundworms	0 (0)	T (12)	T (10)	0 (0)	T (5)
Miscellaneous	T (100)	T (100)	T (100)	T (100)	T (100)

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Literature Cited

Bailey, V. 1932. Mammals of New Mexico. N. Amer. Fauna 53: 1-412.
Borell, A., and R. Ellis. 1934. Mammals of the Ruby Mountains region of northeastern Nevada. J. Mammal. 15: 12-44.
Brower, J. E., and T. J. Cade. 1966. Ecology and physiology of *Napaeozapus insignis* and other woodland mice. Ecology 47: 46-63.
Brown, L. N. 1967. Seasonal activity patterns and breeding of the western jumping mouse (*Zapus princeps*) in Wyoming. Amer. Midl. Nat. 78: 460-470.
———. 1970. Population dynamics of the western jumping mouse (*Zapus princeps*) during a four-year study. J. Mammal. 51: 651-658.
Cary, M. 1917. Life zone investigations in Wyoming. N. Amer. Fauna 42: 460-470.
Craighead, J., and F. Craighead. 1952. Vegetation types of the Jackson Hole Wildlife Park. Unpublished.
Davis, W. E. 1939. The Recent Mammals of Idaho. The Caxton Printers, Ltd., London. 400 p.
Dice, L. R. 1943. The biotic provinces of North America. Univ. Mich. Press, Ann Arbor. 78 p.
Grinnell, J., J. Dixon, and J. M. Linsdale. 1930. Vertebrate natural history of a section of northern California through the Lassen Peak Region. Univ. Calif. Publ. Zool. 35: 1-594.
Hall, E. R., and K. Kelson. 1959. The mammals of North America. New York, The Ronald Press. 1083 p.
Kellogg, L. 1961. Report upon mammals and birds found in portions of Trinity, Siskiyou and Shasta counties, California. Univ. Calif. Publ. Zool. 12: 335-398.
Krutzsch, P. H. 1954. North American jumping mice (genus *Zapus*). Univ. Kansas Publ. Mus. Natur. Hist. 7: 349-372.
Linsdale, J. J. 1938. Environmental responses of vertebrates in the Great Basin. Amer. Midl. Nat. 19: 1-206.
Long, C. A. 1965. The mammals of Wyoming. Univ. Kansas Publ. Mus. Natur. Hist. 14: 493-758.
Moore, A. W. 1928. *Zapus princeps princeps* in Utah. J. Mammal. 18: 103.
Negus, N. C., and J. S. Findley. 1959. Mammals of Jackson Hole, Wyoming. J. Mammal. 40: 371-381.
Quimby, D. C. 1951. The life history and ecology of the meadow jumping mouse, *Zapus hudsonius*. Ecol. Monogr. 21: 61-95.

Reed, J. F. 1952. The vegetation of the Jackson Hole Wildlife Park, Wyoming. Amer. Midl. Nat. 48:700-729.
Sheldon, C. 1934. Studies of the life histories of *Zapus* and *Napaeozapus* in Nova Scotia. J. Mammal. 15:290-300.
Svihla, R. D. 1931. Mammals of the Uinta Mountain Region. J. Mammal. 12: 256-266.
Whitaker, J. O., Jr. 1963. A study of the meadow jumping mouse, *Zapus hudsonius* (Zimmerman), in Central New York. Ecol. Monogr. 33: 215-254.

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Some Cladocera and Copepoda from the Upper Klamath River Basin

Literature showing the occurrence and distribution of Cladocera and Copepoda in Oregon is sparse (Brooks, 1957; Coker, 1943; Kincaid, 1953; Light, 1938; Marsh, 1933; Pearse, 1905; Wilson, 1941; Wilson, 1956a; Wilson and Light, 1951). This paper shows the occurrence and distribution of some species of Cladocera and Copepoda in the Upper Klamath River Basin which overlaps from Oregon into California. A detailed description of the Klamath River Basin and its water resources is given in Bulletin No. 83 (1964) of the Department of Water Resources, State of California.

The habitats sampled include springs, reservoirs, lakes, creeks, rivers, canals, sumps, sloughs, and an ox-bow (Fig. 1). One sampling site, Miller Lake, is not shown on the map of the study area. Miller Lake is about 50 miles north of Upper Klamath Lake and due west of Diamond Lake.

Two-hundred and fifty samples, collected from 25 different areas during 1963-1966, were analyzed for Cladocera and Copepoda. The samples were collected with a variety of different sizes and meshes of plankton nets. All specimens were killed in 10 percent formalin and preserved in 80 percent alcohol. Species of Cladocera and Copepoda were identified with the aid of keys by Brooks (1957, 1959), Pennak (1953), Wilson (1959), and Yeatman (1944, 1959).

Thirty-one species of Cladocera and 28 species of Copepoda (ten Calanoida, seven Cyclopoida, five Harpacticoida) were identified. The occurrence of species in various habitats, the number of species collected in each habitat, and the number of samples taken from each habitat are shown in Tables 1 and 2.

The most ubiquitous species were *Chydorus sphaericus, Cyclops vernalis, Eucyclops agilis,* and *Cyclops bicuspidatus thomasi. C. sphaericus* is a cosmopolitan species very common in a variety of aquatic types in most of North America. All of the above cyclopoid species occur in many different aquatic types throughout North America.

Moinia brachiata, Diaptomus nevadensis, and *Daphnia similis* were collected only in the saline water of Alkali Lake and in the Lost River in the area where water was pumped from the lake to the river.

Upper Klamath Lake, the largest and most sampled of the collecting areas, had the longest species list. The second longest list came from the Lost River System where only 12 samples were collected. Most of these species were probably washed into the river from the large and diverse drainage area.

Samples from almost all collecting areas were taken in the limnetic zones which results in small species lists for the mostly littoral cyclopoids and harpacticoids.

TABLE 1. The occurrence of Cladocera and Copepoda in various aquatic habitats south of Klamath Lake, Oregon during 1964-1965.

Species	Aquatic Areas Sampled										
	Clear Lake	Gerber Reser.	Alkali Lake	Tule Lake	Lost River	Klamath River	Stukel Canal	K. Strait	ADY Canal	Lost R. Oxbow	Area of occurrence
Number of samples taken	2	1	9	3	12	5	1	3	1	1	
Leptodora kindti						X					1
Diaphanosoma brachyurum	X					X					2
Daphnia magna				X		X					2
D. similis			X		X						2
D. galeata mendotae		X								X	2
D. retrocurva	X				X						2
D. pulex				X	X	X	X	X	X		6
D. schodleri	X					X					2
Simocephalus vetulus					X		X	X			3
Ceriodaphnia quadrangula	X			X		X		X	X		5
Moina brachiata			X								1
Bosmina longirostris		X			X	X			X		4
Eurycercus lamellatus					X						1
Leydigia quadrangularus				X	X						2
Alona costata					X						1
Pleuroxus procurvus					X						1
P. denticulatus					X						1
P. aduncus	X				X		X				3
Chydorus sphaericus		X		X	X	X	X	X	X		7
Diaptomus forbesi	X					X		X	X		4
D. nevadensis			X		X						2
D. eiseni						X					1
D. sicilis	X	X	X	X	X	X	X	X			8
D. ashlandi					X	X				X	3
D. novamexicanus								X			1
Eucyclops agilis	X		X	X	X				X	X	6
Cyclops vernalis			X		X	X	X	X		X	6
C. bicuspidatus thomasi	X	X		X	X	X		X		X	7
Mesocyclops leukarti						X					1
Macrocyclops albidus					X		X	X			3
Canthocamptus staphylinoides		X			X				X		3
Total number of species in each area	9	6	6	8	20	15	7	10	7	5	

Acknowledgements

I wish to thank Dr. Charles Hazel, California Department of Fish and Game, Mr. Arthur Gerlach, Oregon Department of Fish and Game, and Mr. William Johnson, Federal Water Pollution Control Administration, for collecting many of the plankton samples.

TABLE 2. The occurrence of Cladocera and Copepoda in Upper Klamath Lake and in aquatic habitats north of Upper Klamath Lake, Oregon during 1963-1964.

Species	Aquatic Areas Sampled														
	Klamath Lake	Miller Lake	Lake of the Woods	Jack Spring	Mare's Egg Spring	Barclay Spring	Geary Sump	7-mile Sump	Tulana E. & W. Sump	Wood River	Williamson River	Geary Canal	Hooper Canal	Algoma Slough	Total areas of occurrence
Number of samples taken	181	9	1	1	2	1	3	1	4	1	2	1	1	1	
Leptodora kindti	X														1
Polyphemus pediculus	X														1
Diaphanosoma brachyurum	X		X												2
Daphnia rosea	X														1
D. galeata mendotae	X	X	X			X									4
D. parvula									X						1
D. pulex	X	X										X			3
D. schodleri	X						X		X					X	4
Simocephalus vetulus	X						X		X						3
S. serrulatus								X							1
Scapholeberis kingi							X	X							2
Ceriodaphnia reticulata	X		X												2
C. lacustris	X														1
C. quadrangula	X							X							2
Bosmina longirostris	X	X					X		X				X		5
Drepanothrix dentata	X														1
Macrothrix laticornis	X														1
Eurycercus lamellatus	X														1
E. glacialis	X														1
A. affinis	X														1
Alona guttata		X													1
Pleuroxus procurvus	X											X			2
P. denticulatus								X							1
P. aduncus								X							1
Chydorus sphaericus	X				X		X	X					X		5
Epischura nevadensis	X													X	2
Diaptomus lintoni	X														1
D. leptopus	X														1
D. clavipes	X														1
D. eiseni	X														1
D. sicilis			X												1
D. ashlandi	X						X							X	3
D. novamexicanus									X						1
Eucyclops speratus								X							1
E. agilis	X		X		X		X	X	X		X				7
Cyclops vernalis	X						X	X	X	X		X	X	X	8
C. capillatus						X									1
C. bicuspidatus thomasi	X						X	X	X					X	5
Macrocyclops albidus	X						X		X		X		X		5
Mesochra rapiens											X				1
Canthocamptus staphylinoides	X														1
Attheyella nordenskioldi					X										1
A. illinoisesis											X				1
A. dogieli				X											1
Total number of species in each area	30	4	5	1	3	2	10	10	9	1	4	3	4	5	

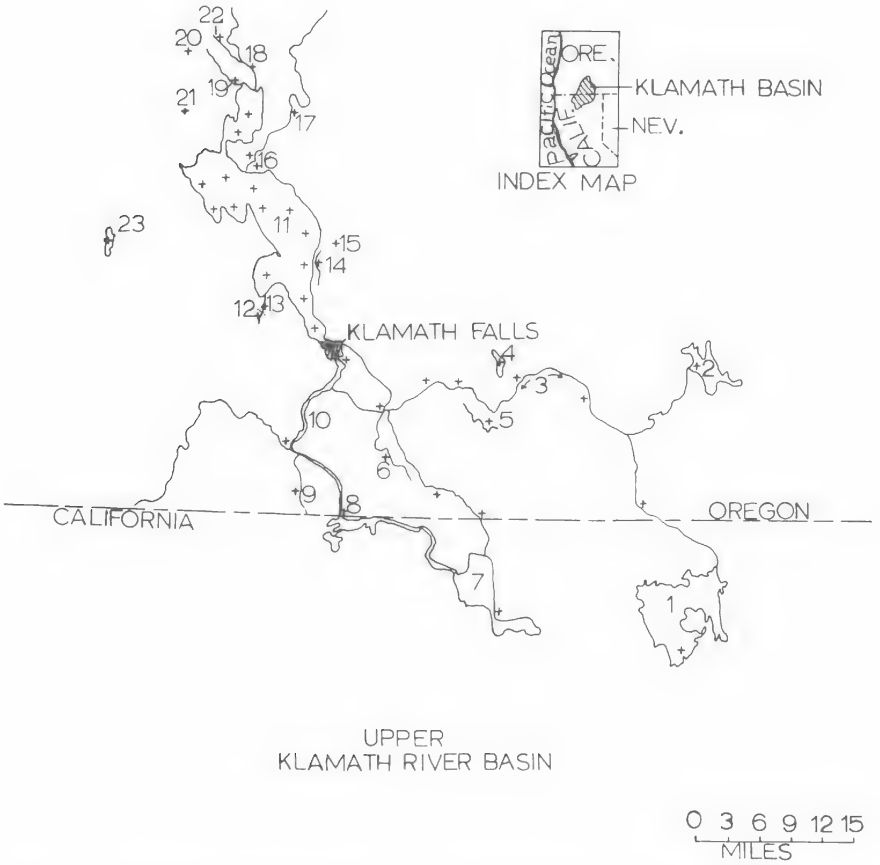

Figure 1. Zooplankton collecting areas in the Upper Klamath River Basin. The numbers correspond to collecting areas as follows: 1. Clear Lake; 2. Gerber Reservoir; 3. Lost River; 4. Alkali Lake; 5. Lost River Oxbow; 6. Stukel Drain; 7. Tule Lake; 8. Klamath Strait Drain; 9. ADY Canal; 10. Klamath River; 11. Upper Klamath Lake; 12. Geary Canal; 13. Geary Sump; 14. Algoma Slough; 15. Barclay Spring; 16. Tulana East and West Sumps; 17. Williamson River; 18. Wood River; 19. 7-mile Sump; 20. Mare's Egg Spring; 21. Jack Spring; 22. Hooper Canal; and, 23. Lake of the Woods. (+ = site sampled).

Literature Cited

Brooks, J. L. 1957. The systematics of North American *Daphnia* Mem. Conn. Acad. Arts Sci. 13: 1-180.

————. 1959. Cladocera. *In* W. T. Edmondson (ed.). Fresh-water Biology. Pp. 587-656. John Wiley and Sons, Inc., N.Y.

Coker, R. E. 1943. *Mesocyclops edax* (S. A. Forbes), *M. leuckarti* and related species in America. J. Elisha Mitchell Sci. Soc. 59: 181-200.

Kincaid, T. 1953. A Contribution to the Taxonomy and Distribution of the American Freshwater Calanoid Crustacea. Privately printed by the author. Calliostoma Co., Seattle.

Light, S. F. 1938. New subgenera and species of diaptomid copepods from the inland waters of California and Nevada. Univ. California Berkeley Publs. Zool. 43: 67-78.

Marsh, C. D. 1933. Synopsis of the calanoid crustaceans, exclusive of the Diaptomidae, found in fresh and brackish waters, chiefly of North America. Proc. U.S. Natl. Mus., 82, art. 18: 1-58.

Pearse, A. C. 1905. Contributions to the copepod fauna of Nebraska and other states. Proc. Am. Microscop. Soc. 26: 145-160.
Pennak, R. W. 1953. Freshwater Invertebrates of the United States. The Ronald Press Co., N.Y. 769 pp.
State of California. 1964. Klamath River Basin Investigation. Resources Agency, Dept. of Water Resources Bull. No. 83. 198 pp.
Wilson, M. S. 1941. New species and distribution records of diaptomid copepods from the Marsh collection in the United States National Museum. J. Wash. Acad. Sci. 31: 509-515.
————. 1956a. North American harpacticoid copepods. 1. Comments on the known freshwater species of the Canthocamptidae. 2. *Canthocamptus oregonensis,* n. sp. from Oregon and California. Trans. Am. Microscop. Soc. 75: 290-307.
————. 1959. Free-living Copepoda: Calanoida. Pp. 738-794. *In* W. T. Edmondson (ed.). Fresh-water Biology, John Wiley and Sons, Inc., N.Y.
————, and S. F. Light. 1951. Descriptions of a new species of diaptomid copepod from Oregon. Trans. Am. Microscop. Soc. 70: 25-30.
Yeatman, H. C. 1944. American Cyclopoid copepods of the *viridis-vernalis* group. (Incl. a Desc. of *Cyclops carolinianus* n. sp.) Amer. Midl. Nat. 32: 1-90.
————. 1959. Free-living Copepoda. Pp. 795-815. *In* W. T. Edmondson (ed.). Freshwater Biology. John Wiley and Sons, Inc., N.Y.

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Toxicity of Kraft Mill Effluent to Selected Estuarine Organisms from Yaquina Bay, Oregon[2,3]

Introduction

An increasing number of pulp mills, using the kraft (sulfate) process to make paper, are being located near or on estuaries. Effects of waste products from these mills on estuarine organisms have not been thoroughly investigated. Most bioassay work with kraft mill effluent (KME) has been performed on various species of salmon (*Oncorhynchus*) (Alderdice and Brett, 1957; Holland *et al.,* 1960). Experiments on avoidance reactions of chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), and steelhead trout (*Salmo gairdneri*) to KME were conducted by Jones *et al.* (1956) and Holland *et al.* (1960). The toxicity of various components of KME to selected salmonids, centrarchids, minnows, and aquatic insects also has been investigated (Van Horn, Anderson, and Katz, 1949; Haydu *et al.,* 1952; Webb, 1958; Courtright and Bond, 1969).

DeWitt (1963) used a synthetic waste to study the effects of KME on freshwater organisms in artificial streams. Cole (1935) noted that the toxicity of the black liquor from the kraft process was generally decreased by aeration. Experiments on the effects of KME on the pumping rate of the American oyster (*Crassostrea virginica*) were reported by Galtsoff *et al.* (1947). Sprague and McLeese (1968a,b) studied the lethal threshold concentration and toxic mechanisms of bleached KME to juvenile Atlantic salmon (*Salmo salar*) and lobsters (*Homarus americanus*).

In an effort to determine the approximate ranges of toxicity of unbleached KME to selected estuarine organisms, laboratory bioassays were conducted at the Oregon State University Fisheries Laboratory on Yaquina Bay, near Newport, Oregon, from April through September, 1964. This study was part of a research program to develop methodologies for the economic evaluation of water pollution control. Because of a lack of time and equipment, no attempt was made to establish precise toxicity levels of KME to the species studied, but median tolerance limits (TL_m's) were estimated for white seaperch (*Phanerodon furcatus*), striped seaperch (*Embiotoca lateralis*), kelp greenling (*Hexagrammos decagrammus*), starry flounder (*Platichthys stellatus*), English sole (*Parophrys vetulus*), and Dungeness crab (*Cancer magister*). Information on preliminary bioassays is reported for pile perch (*Rhacochilus vacca*) and walleye surfperch (*Hyperprosopon argenteum*).

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Materials and Methods

Laboratory Procedures

With a few exceptions, laboratory bioassay procedures were patterned after those suggested by Doudoroff *et al.* (1951). Bioassays were conducted in 18 liters of standing sea water mixed with KME to some predetermined percentage. Contrary to the recommendations of Doudoroff *et al.* (1951), all test solutions were aerated. Aeration was necessary because of a higher ratio of fish mass to water volume than that suggested by Doudoroff *et al.* (*ibid*). Aquaria were wide-mouth, five-gallon, glass jars. Experiments were conducted in a dark, constant temperature room at 19 $\pm$ 2° C.

Samples for chemical analyses were obtained every 24 hours, just before solutions in the aquaria were changed and at the end of the test period. Salinity samples were taken from control aquaria only.

Salinity determinations were made with hydrometers and corrected for temperature.

Determinations of dissolved oxygen concentrations were according to the Alsterberg (Azide) modification of the Winkler method (American Public Health Assoc., 1960). There are substances in the KME waste that interfere with the oxygen determination by the modified Winkler method and produce lower oxygen values than actually exist in the solutions (Breese, 1965; DeWitt, 1963). The exact amount of interference has not been established; however, the modified Winkler method was the best method available for determining dissolved oxygen concentrations in waste solutions containing KME.

Hydrogen ion concentrations were determined with a battery-operated, Model N-2, Beckman pH meter.

Biological Procedures

Results of an angler-catch survey indicated the five most frequently caught fishes in Yaquina Bay were white seaperch, striped seaperch, pile perch, starry flounder, and kelp greenling. These species and the Dungeness crab were used in bioassay tests. In addition, the young of walleye surfperch and English sole were used as test animals because of small size and availability.

Test Specimens

Both vertebrate and invertebrate test specimens were obtained from Yaquina Bay. Captured fish were retained in a 250-gallon holding tank supplied with water pumped from the bay. Crabs were held near the laboratory in submerged wire cages attached to a floating dock. All specimens were fed while in holding tanks or cages.

Both fishes and invertebrates were held at temperatures lower than that of the experimental media. Test specimens were acclimated to experimental conditions by placing them in aquaria with water of the same temperature as that in the holding tank and allowing the water to warm to room temperature (19 $\pm$ 2° C) over two or three days. Doudoroff *et al.* (1951) suggested that test organisms be acclimated for at least 10 days. Lack of suitable aquaria and laboratory space limited the time for acclimation. Specimens were not fed during acclimation or test periods.

Kraft Mill Effluent

Kraft mill effluent (KME) designates an alkaline waste from the manufacture of paper produced by the digestion of certain types of wood with a strong caustic solution containing sodium hydroxide, sodium carbonate, and sodium sulfide (Shreve, 1956).

Samples from the strong and weak effluent streams of an unbleached kraft mill were collected separately by automatic sampling devices. The strong effluent was composed of blow and reflief condensates, contaminated evaporator condensates, boiler blowdown water, and pump and agitator gland seepage. Contents of the weak effluent were composed of cooling water from compressors, "white water" from paper waste, seal water from vacuum pumps, and roof drain and wash-up water. Each week the composite samples were brought to our laboratory. The samples of strong waste were stored in stoppered glass containers out of direct sunlight. The weak waste was stored out of direct light in open, wide-mouth, five-gallon jars.

Flows for each seven-day period were supplied by the sampled kraft mill. Using these figures, the strong-waste, weak-waste, and freshwater fractions were combined to form a total waste representative of the probable effluent that the mill would discharge if all wastes were placed directly into the bay at one point.

Salt water was added to the test solutions in place of the freshwater fraction to keep the salinity as high as possible in high percentage KME tests. This was done to prevent placing an extra stress on the test organisms because of lowered salinities that would result if freshwater were used as a diluent.

Control solutions were composed of salt water mixed with freshwater equal in amount to the combined strong- and weak-waste components in the highest test concentration. Thus, test organisms in the control solution would be subjected to the same decrease in salinity as those in the strongest waste concentration and should reflect any direct effects of reduced salinity.

Bioassay Procedures

All bioassays were conducted for 96 hours or until more than 50 percent of the test organisms died. Dissolved oxygen levels were maintained at five ppm or higher in most test solutions. No attempt was made to test the effects of dissolved oxygen concentrations on fish survival; however, KME usually has a high chemical toxicity before the biochemical oxygen demand would greatly affect the oxygen supply (McKee and Wolf, 1963; Waldichuk, 1962).

Preliminary tests were conducted for each species to determine the approximate upper and lower limits of toxicity of KME. The lower limit was defined as the highest concentration where more than 50 percent of the organisms lived for 96 hours. The upper limit was defined as that concentration where more than 50 percent of the organisms died within 24 hours. After these two values were determined, they were marked on a log scale. The distance between the points was divided into equal sections based on the number of concentrations to be tested. This method was not used with the starry flounder, English sole, and Dungeness crab. For these species, concentrations were increased by five or 10 percent from the predetermined lower value to the upper value according to the range to be tested.

Test organisms chosen for final tests were the smallest available. Average lengths and weights are given in Table 1. When available, 20 specimens were used per test concentration, the fish being equally divided into two jars per concentration. If sufficient fish (20) were not available, the greatest number on hand was used.

All test and control solutions were renewed every 24 hours to prevent possible detoxification of the waste by the test organisms or by aeration, which could result in a

TABLE 1. Weights and sizes of test organisms used in bioassays of KME toxicity.

Species	Weight (grams)			Length (millimeters)			Remarks
	Max.	Min.	Av.	Max.	Min.	Av.	
Starry flounder	50.0	2.2	22.1	190.0	58.0	102.8	total length
White seaperch	----	----	----	76.0	57.0	67.6	fork length
Dungeness crabs							
small size	44.8	3.2	10.3	65.0	26.0	37.2	"length" is
large size	136.0	76.0	112.1	100.5	78.0	90.5	carapace width
Striped seaperch	14.9	6.6	9.5	97.0	78.0	87.3	fork length
Kelp greenling	22.1	3.5	12.2	130.0	75.0	105.0	total length
English sole	----	----	----	80.0	62.0	72.2	total length

higher 48- or 96-hour TL_m. All dead animals were removed from the test containers and their number recorded as soon as observed.

The median tolerance limit (TL_m) represents the theoretical concentration of a toxic substance at which 50 percent of the test organisms survive. A TL_m was derived for each species by straight-line graphical interpolation after the method recommended by Doudoroff *et al.* (1951) and American Public Health Association (1960).

Results

Based on the final bioassays, the daily survival and daily median tolerance limits (TL_m's) for each species are presented in Table 2. The TL_m for white seaperch was 17.0 percent KME in 48 hours and 10.6 percent KME in 96 hours. All white seaperch died within 12 hours in the 32.0 percent concentration.

Results for striped seaperch were similar to those for white seaperch. The 48-hour TL_m was 17.3 percent and the 96-hour TL_m was 9.6 percent KME (Table 2). Two out of 10 (20 percent) of the control specimens died. Since there were no mortalities in the 4.0 percent concentration, the test was considered to be valid.

Starry flounder had a 48-hour TL_m of 25.0 percent KME and a 96-hour TL_m of 12.2 percent (Table 2). Ninety-four percent of the flounder lived for 96 hours in the 5.0 percent concentration of KME. Seventy-eight percent of the flounder lived for over 24 hours in the 50.0 percent concentration.

All English sole lived in a 5.0 percent concentration of KME but none survived in the 30.0, 40.0, and 50.0 percent concentrations. No sole lived over 72 hours in the 20.0 percent concentration. The 48-hour TL_m for English sole was 18.7 percent and the 96-hour TL_m was 8.5 percent KME (Table 2).

Kelp greenling had a 48-hour TL_m of 31.0 percent KME and a 96-hour TL_m of 15.2 percent (Table 2). Even with concentrations as high as 35.0 percent KME, there were insufficient mortalities to establish a 24-hour TL_m. In the 35.0 percent concentration, fish survived over 48 hours but all were dead by the end of 72 hours.

Dungeness crabs were the least affected by the KME tested. KME concentrations up to 50.0 percent produced no mortality of adult crabs and only a 6.0 percent mortality of small crabs. A mortality of 18.0 percent occurred in the control group of

TABLE 2. Daily percent survival of species in various concentrations of KME, and daily median tolerance limits of KME for each species.

Species	Time (hrs)	Percent Survival at % Concentration of KME						TL_m (% KME)	Percent Survival of Control
		6.0	*9.4*	*14.0*	*21.0*	*32.0*			
White	24	100	100	100	94	0		26.0	100
Seaperch	48	94	100	61	39	0		17.0	100
(N = 18)	72	89	83	28	6	0		11.9	100
	96	83	72	0	0	0		10.6	100
		4.0	*6.0*	*9.0*	*13.0*	*20.0*			
Striped	24	100	100	100	100	100		---	100
Seaperch	48	100	90	90	100	20		17.3	100
(N = 10)	72	100	80	90	10	0		11.0	90
	96	100	80	60	0	0		9.6	80
		5.0	*10.0*	*20.0*	*30.0*	*40.0*	*50.0*		
Starry	24	100	100	94	100	89	78	88.5	100
Flounder	48	100	94	72	30	0	0	25.0	94
(N = 18)	72	100	89	22	0	0	0	15.0	94
	96	94	67	6	0	0	0	12.2	94
		5.0	*10.0*	*20.0*	*30.0*	*40.0*	*50.0*		
English	24	100	100	100	0	0	0	24.5	100
Sole	48	100	95	45	0	0	0	18.7	100
(N = 20)	72	100	75	0	0	0	0	12.6	100
	96	100	35	0	0	0	0	8.5	100
		8.0	*12.0*	*17.0*	*24.0*	*35.0*			
Kelp	24	90	90	100	70	80		---	100
Greenling	48	80	90	80	70	40		31.0	100
(N = 10)	72	80	80	70	40	0		21.4	100
	96	80	70	40	0	0		15.2	100
					30.0	*40.0*	*50.0*		
Dungeness	24				100	100	100	---	94
Crabs	48				100	100	100	---	88
(N = 17	72				100	100	94	---	82
small)	96				100	100	94	--	82

small crabs (Table 2). Some of the small crabs molted while in the test aquaria and were unable to defend themselves while their exoskeletons hardened. Therefore, mortalities of small crabs were thought to be primarily due to cannibalism rather than KME toxicity, since crabs with soft exoskeletons were able to survive if not attacked.

Preliminary bioassay data only were determined for walleye surfperch and pile perch. A lack of sufficient numbers of test specimens prevented refined bioassay test results for these two species. Tests of five walleye surfperch per aquarium were conducted in concentrations of 4.0, 8.0, 16.0, and 32.0 percent KME. No fish survived for 24 hours in the 32.0 percent concentration. In the 16.0 percent concentration, all fish were dead within 48 hours and no fish lived for 72 hours in the 8.0 percent solution. Therefore, the 48-hour TL_m was approximately 11.0 percent, and the 96-hour TL_m was approximately 5.0 percent.

Groups of six or seven pile perch were subjected to preliminary tests in two different weekly samples of KME. In one sample of waste in concentrations of 4.0, 8.0, 16.0, and 32.0 percent, all fish in the 32.0 percent concentration died in less than 48 hours, but all fish survived for 48 hours in the 16.0 percent concentration. A second series of KME concentrations of 16.0, 20.0, and 30.0 percent was tested with groups of

eight pile perch. In this series no fish lived over 48 hours in any of the KME solutions. These results emphasize variations in KME toxicity that can occur.

Because there was no apparent correlation of the information on chemicals with the final survival figures, a detailed analysis of the chemical data is omitted. The range of chemical data for all final tests was a follows: salinity, 20.0-31.8 ppt; pH, 7.6-8.1; and dissolved oxygen, 4.4-8.2 mg/1 with most values ranging between 6.0 and 8.0 mg/1.

Discussion

Several problems were encountered during conduct of the bioassays. The final test on starry flounder required a large quantity of KME. Therefore, to insure enough effluent from one weekly sample for the complete 96-hour test, the fish in the 20 percent and 30 percent concentrations in the two test series conducted (both series conducted simultaneously) were placed into one aquarium for each concentration when the total number of surviving fish in the same waste concentration numbered 10 or fewer.

When testing Dungeness crabs at 50.0 percent concentrations of KME, it was difficult to maintain a high level of dissolved oxygen. Attempts to increase the level of dissolved oxygen in the aquaria by increasing the rate of aeration produced a vigorous foaming action. The foam increased until it flowed out of the aquaria. Waldichuk (1962) noted that salt water tended to enhance the frothing action of some of the black liquor constituents of KME. If foaming was allowed to continue, the KME solution in the aquaria turned a lighter color and a soapy black scum would form on the outside of the aquaria.

Breese (1964) used bay mussel larvae (*Mytilus edulis*) to test the toxicity of the dried foam and the liquid residue. He concluded that the dried form was more toxic than the liquid residue produced by violent aeration. Additional testing showed a substantial loss of toxicity of the original KME concentration when the wet foam was not returned to the waste. In order to prevent excess foaming in our aquaria, the aeration rate was reduced which resulted in the lowered levels of dissolved oxygen. Because all adult crabs and 94 percent of the young survived 96 hours in 50 percent KME, the lowered D. O. did not appear harmful to the test organisms.

While conducting bioassays on the selected estuarine species, we did not conduct simultaneous tests with the same effluent on a standard test fish. Consequently, the bioassay results for each species of fish cannot be compared, and we had no way to measure small changes in the toxicity of weekly samples of KME. The test results reported, however, should be in the approximate toxicity range for each species tested because: (1) the final test results were near the toxicity levels indicated by the preliminary tests; (2) according to the pulp mill laboratory personnel, there were no changes in mill operation that would greatly affect the composition or toxicity of the waste; (3) of all the samples of KME used in bioassays on fin-fish, only one sample had a toxicity level that seemed to be appreciably higher than the other samples. That sample was used in the preliminary test on pile perch and was easily detected. Even when the daily waste samples were combined to one weekly sample, a wide range of toxicity was noticed in this instance. Researchers should be alerted to check for wide ranges in the toxicity of KME.

Another factor affecting the TL_m's was aeration of the waste in the aquaria. Aeration may have removed some of the toxic, volatile components present in the waste which would increase the TL_m's for the species tested. However, the test results using aerated KME should be indicative of the effects of KME on fish populations in Yaquina Bay because: (1) the strong effluent from the kraft mill is aerated as it is pumped into storage lagoons. From the open lagoons the waste would be pumped to the bay; (2) after entering the estuary, the waste must travel through several tidal cycles and for a distance of 9 to 12 nautical miles before reaching the ocean. Yaquina Bay is classed as a well-mixed estuary from August through November (Burt and McAlister, 1959), and KME wastes should be well exposed to sunlight and air. By the time such wastes reached areas where substantial populations of fish exist, the toxicity of the more stable components should be more important as a factor affecting the populations of fish than the unstable components present in the discharge.

Toxicity values of aerated KME may be more indicative of conditions that would occur up or down bay from the discharge point of the kraft mill than the toxicity values established from a waste that contained all of its volatile components. The toxicity values expressed here should give a useful indication of the possible effects of KME on the more important estuarine organisms of Yaquina Bay.

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Literature Cited

Alderdice, D. F., and J. R. Brett. 1957. Some effects of kraft mill effluent on young Pacific salmon. J. Fish. Res. Bd. Can. 14: 783-795.

American Public Health Association. 1960. Standard Methods for the Examination of Water and Waste Water. 11th ed. New York. 626 pp.

Breese, W. P. 1964. Unpublished research on the effects of foaming on the toxicity of kraft mill effluent and on the toxicity of kraft mill effluent to a species of estuarine algae. Newport, Oregon. Marine Laboratory, Dept. Fish and Wildl., Oregon State University.

————. 1965. Assistant Professor of Fisheries, Department of Fisheries and Wildlife. Oregon State University. Personal communication. Corvallis, Oregon.

Burt, W. V., and W. B. McAlister. 1959. Recent studies in the hydrography of Oregon estuaries. Oregon Fish Commission. Res. Briefs 7: 168-184.

Cole, A. E. 1935. Water pollution studies in Wisconsin. Effects of industrial pulp and paper mill wastes on fish. Sew. Works J. 7: 280-302.

Courtright, R. C., and C. E. Bond. 1969. Potential toxicity of kraft mill effluent after oceanic discharge. Progressive Fish-Cult. 31: 207-212.

DeWitt, J. W., Jr. 1963. Effects of Pollutional Conditions on Stream Organisms with Especial Emphasis on Stonefly Naiads. Ph.D. thesis. Corvallis, Oregon State University. 216 pp.

Doudoroff, P., B. G. Anderson, G. E. Burdick, P. S. Galtsoff, W. B. Hart, R. Patrick, E. R. Strong, E. W. Surber, and M. W. Van Horn. 1951. Bio-assay methods for the evaluation of acute toxicity of industrial wastes to fish. Sewage and Ind. Wastes 23: 1380-1397.

Galtsoff, P. S., W. A. Chipman, Jr., J. B. Engle, and H. N. Calderwood. 1947. Ecological and physiological studies on the effect of sulfate pulp mill wastes on oysters in the York River, Virginia. U.S. Fish and Wildl. Serv. Fish. Bull. 51: 59-186.

Haydu, E. P., H. R. Amberg, and R. E. Dimick. 1952. The effect of kraft mill waste components on certain salmonid fishes of the Pacific Northwest. TAPPI 35: 545-549.

Holland, G. A., J. E. Lasater, E. D. Neumann, and W. E. Eldridge. 1960. Toxic Effects of Organic and Inorganic Pollutants on Young Salmon and Trout. Seattle. Wash. Dept. Fish. Res. Bull. No. 5. 264 pp.
Jones, B. F., C. E. Warren, C. E. Bond, and P. Doudoroff. 1956. Avoidance reactions of salmonid fishes to pulp mill effluents. Sewage and Ind. Wastes 28: 1403-1413.
McKee, J. E., and H. W. Wolf. 1963. Water Quality Criteria. 2d. ed. Sacramento (California State Water Quality Control Board. Publication No. 3-A). 548 pp.
Shreve, R. N. 1956. The Chemical Process Industries. McGraw-Hill Inc., New York. 1004 pp.
Sprague, J. B., and D. W. McLeese. 1968a. Toxicity of kraft pulp mill effluent for larval and adult lobsters, and juvenile salmon. Water Res. 2: 753-760.
———. 1968b. Different toxic mechanisms in kraft pulp mill effluent for two aquatic animals. Water Res. 2: 761-765.
Van Horn, M., J. B. Anderson, and M. Katz. 1949. The effect of kraft pulp mill wastes on some aquatic organisms. Trans. Amer. Fish. Soc. 79: 55-63.
Waldichuk, M. 1962. Some water pollution problems connected with the disposal of pulp mill wastes. Can. Fish. Cult. No. 31: 3-34.
Webb, W. E. 1958. Preliminary Studies To Determine the Nature of the Principal Toxic Constituents of Kraft Pulp Mill Wastes. Master's thesis. Corvallis. Oregon State College. 55 pp.

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Susceptibility of Ponderosa, Jeffrey, and Lodgepole Pines to Pocket Gophers

Pocket gophers (*Thomomys* spp.) occupy many acres of wild land in the western states, and much has been written about their activities on meadows and rangelands (Ellison and Aldous, 1952; Hansen and Ward, 1966; Howard and Childs, 1959; Julander *et al.,* 1959; Moore and Reid, 1951). Gophers are also widely distributed on western forests and are known to damage and kill several conifer species (Barnes *et al.,* 1970; Dingle, 1956; Hermann and Thomas, 1963; Moore, 1940; Tevis, 1956).

Relatively little is known about gophers on forest land, or their response to environmental modifications resulting from wildfire or timber management practices. Hermann and Thomas (1963) reported that gophers were a major cause of losses in a ponderosa pine (*Pinus ponderosa*) plantation in southern Oregon. Recently, intensified observations by foresters have confirmed that gophers are severely damaging seedlings and saplings on many national forests in the Pacific Northwest (Crouch, 1969). Part of this apparent increase in gopher damage is a consequence of more frequent and systematic plantation examinations. Also important is the recognition that some of the damage to smaller trees formerly attributed to porcupines (*Erethizon dorsatum*) may have been caused by gophers (Crouch, 1969).

Operational efforts to protect conifers from gophers have been limited to reduction of animal numbers by trapping or poisoning. Trapping appears impractical considering the vast acreages needing protection, and application of poisoned bait by hand is slow and results are variable. Moreover, frequent treatment appears necessary since repopulation is virtually certain (Dingle, 1956; Hermann and Thomas, 1963). A mechanical bait-dispenser is now being tested (Barnes *et al.,* 1970; Canutt, 1970); but, even if judged effective, this too will undoubtedly require repeated use and be limited in applicability by edaphic and topographic site factors. Long-lasting protection, preferably without harming animals or their habitat, is needed.

Some foresters working in south-central Oregon observed that ponderosa pines seemed to be more heavily damaged by gophers than Jeffrey pines (*P. Jeffreyi*) or lodgepole pines (*P. contorta*). If these observations could be substantiated, then the less-susceptible species might be planted in gopher-infested areas where the ecological requirements of the tree were met. The purpose of this study was to determine relative preferences of gophers for the three pine species on one area where damage by gophers was known to occur.

Study Area and Methods

The study was conducted on a portion of the Cave Mountain Burn, near the town of Chiloquin, in south-central Oregon. The site, located about 4000 ft. in elevation, had been well stocked with ponderosa pine and bitterbrush (*Purshia tridentata*) until the pines and most of the shrubs were destroyed by wildfire in 1959 (Fig. 1). During the study, vegetation was dominated by western needlegrass (*Stipa occidentalis*), with lesser amounts of other grasses and a few forbs and shrubs, totaling about 40 percent crown cover (Fig. 2).

Ponderosa pines were planted on most of the burn in 1962 and 1963, but few remained by 1966, mainly because of intensive gopher depredations. Many of the survivors bore scars from gopher gnawing, and freshly killed seedlings were readily observed (Fig. 2). Gopher mounds were abundant, and the upper soil layers were mined with burrows.

Figure 1. Patch of unburned timber near the study area, July 1970. This site was probably swept by ground fire in 1959.

Figure 2. Typical burned area adjacent to the study site, March 1966. Trees marked by cards were planted in 1962, damaged by gophers during the 1965-66 winter, and subsequently died.

For this study, 90 seedlings—30 each of ponderosa, Jeffrey, and lodgepole pine—were randomly planted in each of four adjacent blocks. All trees were 2-0 stock grown at the U.S. Forest Service nursery at Bend, Oregon. Seeds for the ponderosa and lodgepole pines had been locally collected, but the Jeffrey pine seed source was many miles southwestward, across the crest of the Cascade Range. The 360 seedlings were auger-planted at 8-by-8-ft. spacings and individually marked with wooden stakes. Trees were planted in March 1966 and examined in April, July, and September each year through 1969.

Results and Discussion

Losses to gophers began almost immediately—several trees were pulled into burrows within three hours after planting. By September 1969, two-thirds of all trees had been destroyed by gophers (Table 1). Losses among species were nearly identical. Survival

of undamaged seedlings of all species was high, but nonanimal losses might have been greater if gophers had not decimated the stock.

Although gophers killed trees during all seasons, the major losses occurred during winter, presumably under snow (Table 2). Two midwinter examinations were made

TABLE 1. Mortality of planted ponderosa, Jeffrey, and lodgepole pines, March 1966 through September 1969.

Pine species[1]	Mortality cause		
	Gophers	Other	Total
	Percent of trees planted		
Ponderosa	67.5[2]	2.5[2]	70.0[2]
Jeffrey	66.7	7.5	74.2
Lodgepole	65.0	9.2	74.2

[1] One-hundred and twenty trees of each species were planted.
[2] Species means are not significantly different at the 5 percent probability level.

TABLE 2. Seasonal pattern of gopher mortality in planted ponderosa, Jeffrey, and lodgepole pines, March 1966 through September 1969.

Time interval	Mortality from gophers[1]	
	Percent of trees remaining	Cumulative percent of trees planted
March 1966 - April 1966	5.8	5.8
May 1966 - Sept. 1966	1.8	7.5
Oct. 1966 - April 1967	40.9	44.2
May 1967 - Sept. 1967	5.3	46.9
Oct. 1967 - April 1968	38.7	65.6
May 1968 - Sept. 1968	1.8	66.1
Oct. 1968 - April 1969	1.0	66.4
May 1969 - Sept. 1969	0.0	66.4

[1] Three-hundred and sixty trees were planted.

during snow-free periods. By late December 1966, about one-quarter of the total winter damage sustained that year had occurred. By February 1968, gophers had taken two-thirds of the total number of trees destroyed during the 1967-68 winter. Periodic inspections from June through September each year indicated that summer damage was about evenly distributed through the season.

The same seasonal damage patterns were observed each year, but the relative intensities of losses varied from year to year. Gophers destroyed 44 percent of the seedlings during the first year after planting, 41 percent of the remainder the second year, but only 3 percent of surviving trees in the third year.

During the study, three kinds of pocket gopher damage were observed: (1) Trees missing from their planting site accounted for 76 percent of the losses. Excavation at or near the planting hole nearly always revealed a main gopher burrow or lateral tunnel through which the tree had been removed. (2) Tops were removed at or just below the soil surface in 14 percent of the losses. (3) Roots were severed and removed and the rootless tops left standing in 10 percent of the gopher-killed trees. All seedlings injured by gophers subsequently died. Excavation of a sample of surviving trees at the final examination revealed no root damage.

No more than six adjacent trees were taken by gophers during one season of any year. The animals appeared to harvest seedlings singly or in small groups.

Results showed that planting one pine species instead of another did not reduce gopher predation. The findings also clearly demonstrated that gophers damaged conifers predominantly during the winter which suggests that efforts to control damage by reducing gopher numbers should be scheduled just before winter. Finally, the loss rate to gophers over the three-year study confirms the prediction by others that unless trees are protected from these animals, plantations infested with them are probably doomed (Dingle, 1956; Hermann and Thomas, 1963).

Literature Cited

Barnes, V. G., Jr., P. Martin, and H. P. Tietjen. 1970. Pocket gopher control on Oregon ponderosa pine plantations. J. Forest. 68(7): 433-435.

Canutt, P. R. 1970. Development and operation of the forestland burrow builder, p. 77-79. *In* Wildlife and Reforestation in the Pacific Northwest Symp. Proc. Oreg. State Univ., Corvallis, Oreg.

Crouch, G. L. 1969. Animal damage to conifers on National Forests in the Pacific Northwest Region. Pac. Northwest Forest & Range Exp. Sta., U.S.D.A. Forest Serv. Resource Bull. PNW-28. 13 p.

Dingle, R. W. 1956. Pocket gophers as a cause of mortality in eastern Washington pine plantations. J. Forest. 54(12): 832-835.

Ellison, L., and C. M. Aldous. 1952. Influence of pocket gophers on vegetation of subalpine grassland in central Utah. Ecology 33(2): 177-186.

Hansen, R. M., and A. L. Ward. 1966. Some relations of pocket gophers to rangelands on Grand Mesa, Colorado. Colo. Agr. Exp. Sta. Tech. Bull. 88. 20 p.

Hermann, R. K., and H. A. Thomas. 1963. Observations on the occurrence of pocket gophers in southern Oregon pine plantations. J. Forest. 61(7): 527-529.

Howard, W. E., and H. E. Childs, Jr. 1959. Ecology of pocket gophers with emphasis on *Thomomys Bottae Mewa.* Hilgardia 29(7): 277-358.

Julander, O., J. B. Low, and O. W. Morris. 1959. Influence of pocket gophers on seeded mountain range in Utah. J. Range Manage. 12(5): 219-224.

Moore, A. W. 1940. Wild animal damage to seed and seedlings on cutover Douglas-fir lands of Oregon and Washington. U.S. Dep. Agr. Tech. Bull. 706. 28 p.

————, and E. H. Reid. 1951. The Dalles pocket gopher and its influence on forage production of Oregon mountain meadows. U.S. Dep. Agr. Circ. 884. 36 p.

Tevis, L., Jr. 1956. Pocket gophers and seedlings of red fir. Ecology 37(2): 379-381.

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Pollen Size Variation in Some Western North American Pines as Related to Fossil Pollen Identification

Pines produce a distinctive vesiculate pollen grain which is easily identifiable in the fossil pollen record. Unfortunately, differences among pollen grains produced by different pine species are not so discernible, often causing the pollen of several pine species to be considered in fossil pollen diagrams as an undifferentiated group. In view of the large variation in ecologic amplitudes among pines, this lack of persistent differences among species' pollen has frustrated attempts to construct Quaternary vegetation and climatic history in a more satisfactory manner. For example, in northwestern United States *Pinus ponderosa* Laws. and *P. contorta* Dougl., two diploxylon pines, not only have different ecologic amplitudes, but also may differ markedly as to their role in the community: *P. ponderosa* can occur as either a climax or a seral dominant; *P. contorta* is commonly seral, and is less commonly a climax dominant (Daubenmire and Daubenmire, 1968; Franklin and Dyrness, 1969). Interpretations of past climate and plant community composition thus might vary greatly depending upon whether pollen of one or the other (or both) of these species could be identified at a given time in the fossil record.

In western North America specific identifications of fossil pine pollen have involved several approaches. Bright (1966), in study of the pollen record at Swan Lake in southeastern Idaho, eliminated from consideration several pines (*e.g., P. monticola* Dougl. and *P. ponderosa*) which are not common there today. Fossil pine pollen was divided between the two remaining pines in the region (*P. contorta* and *P. flexilis* James) on the basis of distal verrucae. Baker (1970) used the apparent absence of *P. ponderosa* in Yellowstone Park during postglacial time, as well as macrofossil evidence, to identify pollen in the fossil record there as *P. contorta.*

Both Hansen (1947) and Ting (1966) have proposed methods to identify specific pine pollen types through measurement of one or more dimensions on the pollen grain. Ting's method used mainly dimensions and statistics of the corpus in conjunction with an index based on ratios of overall, corpus, and saccus breadth. In contrast, Hansen used a size-range (frequency) distribution for distinguishing the pollen of *P. contorta, P. monticola,* and *P. ponderosa* (Fig. 1). This approach involves initial plotting of the length of the pollen grain (*i.e.,* corpus breadth) versus the number of grains of that size in a 100-grain fresh pollen sample for each pine species in the region. In general, each of his pollen distributions appears as a bell-shaped curve showing the corpus breadth for any modern sample of one pine species to center about a small range of values (Hansen, 1947). Fossil pollen was attributed to a given species when its corpus breadth fell within the known range of one of the modern pine pollen samples. Fossil

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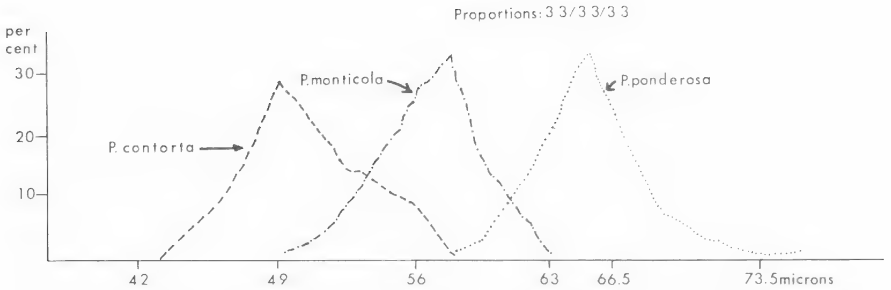

Figure 1. Size-frequency distribution of modern pine pollen as constructed by Hansen (1947).

pollen with a corpus breadth falling in a region of overlap between two modern pollen samples was assigned to an unidentified category. A series of these curves constructed in several areas within northwestern United States and adjacent Canada was used by Hansen (1947) to identify fossil pine pollen. In addition, Hansen (1947) stated that the comparatively larger bladder (saccus) size of *P. ponderosa* pollen aided in its identification.

Similar attempts to identify pine pollen as to species through size frequency or range identification also have been proposed for eastern North America pines by Cain (1940) and Cain and Cain (1944), but have been questioned by Whitehead (1964). Whitehead, after a comprehensive study of the size frequency distribution of pollen representing 13 eastern pines, concluded that the technique in that region had low reliability for reasons which included variation in pollen size throughout the geographic ranges of the species, and inability to compare modern and fossil grains' sizes directly due to possible swelling effects of sediment on fossil pollen.

Deevy (1948) previously had questioned Hansen's use of the technique, because of several apparent uncertainties, but concluded that the validity of Hansen's data probably was not seriously affected. Inability to use this method due to size overlap among the species considered by Hansen has been reported by Terasmae (as cited in Schultz and Smith, 1965) and Bright (1966). Heusser (1960) used Hansen's size-range curves, however, to distinguish between fossil pollen of *P. monticola* and *P. contorta* where their present geographic ranges overlap.

Actually, considerable overlap of size ranges occurs in Hansen's (1947) curves for modern pollen (Fig. 1). Less overlap between *P. contorta* and *P. monticola* pollen sizes is mentioned in an earlier publication (Hansen, 1940), but the size-range curves for these samples were not published. The three curves as produced in Hansen's 1947 monograph (*e.g.,* Fig. 18, page 43) were used to check in a cursory manner the potential accuracy of the size-range method, and to assess the effect of overlapping size ranges on interpretations made from size-range curves. Instead of considering the figure as representing measurements of three separate samples of 100 grains each, it may be treated also as a hypothetical sample of 300 pollen grains for which the proportion contributed by each pine is sought. Pooling of the three samples involves the removal of those areas which are in regions of overlap between any two curves, and the replotting of the grains' measurements which these areas represent. Otherwise, two pollen

grains' measurements can occupy the same position under the curve, and not display the true distribution of sizes for this 300-grain sample.

Rearrangement of the data yields a composite curve (Fig. 2) in which the three peaks are not as distinct as those in Figure 1. The stippled area (from 50-64 μm) in Figure 2 represents the pollen under the composite curve which must be placed in an unidentified category, since it falls within an area of overlap between measurements of the pollen from two different pines. When the remaining areas on either side of the unidentifiable range of measurements are measured, the following proportions of each species appear to be present: *P. contorta*, 34 percent; *P. monticola,* 0 percent; *P. ponderosa,* 66 percent. The accuracy of the percentages depends on the detail to which the original curves were plotted and the exactness of the area determinations. The nature of vegetation inferred from such percentages (when all other sources of error are neglected, *e.g.,* differential pollen production) probably would be a community dominated by *P. ponderosa* with *P. contorta* present. The actual contribution of pollen by the three species (33 percent for each) would go unrecognized. Specific influences of the interpretation based on size-range data from the sample illustrated are given below.

1. Corpus breadth of *P. monticola* pollen is overlapped by both other species, and consequently it is underrepresented in the inferred vegetation.

2. Recognition of *P. ponderosa* versus *P. contorta* thus becomes a function of the amount of *P. monticola* pollen present in the sample, because all pollen of the other two pines can be identified when there is no *P. monticola* pollen in the sample. Unfortunately the amount of *P. monticola* is unknown unless its distal verrucae are used to identify it.

From this example, the following observations may be made concerning the effect of overlap on inferences concerning pollen identified using the size-range method:

1. Use of the size-range method results in underestimation of all pollen of intermediate size (*e.g.,* pollen of *P. monticola* and a considerable amount of *P. contorta* pollen).

2. Such underestimation affects species differentially. No pollen of *P. monticola* could be positively identified in the above example, but sizeable amounts of *P. ponderosa* grains appear to be identified accurately. This is in contrast to the view of Hansen

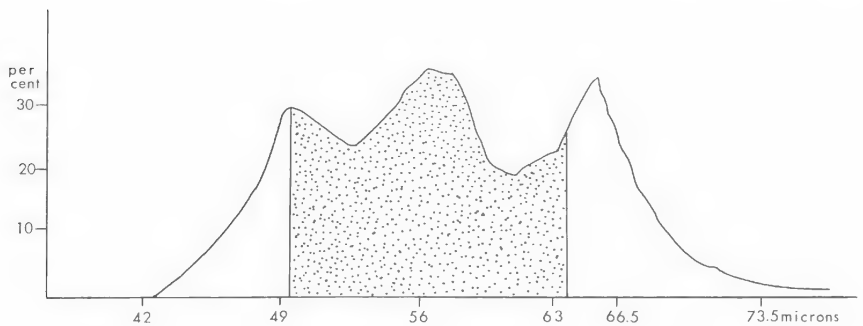

Figure 2. Size-frequency distribution of composite curve based on pooling 300 pollen grain measurements. Stippled area represents material within original areas of overlap.

(1947), who felt the proportion of any species in the identified and unidentified categories was probably the same.

3. The percentage of material in the unidentified category increases with the number of species considered in any series of curves. Had the distributions of several other western pines' pollen been included, an almost indecipherable field of overlap would have developed from the standpoint of size-range determinations.

In view of the problems demonstrated with this technique for eastern pines (Whitehead, 1964), and considering the problems illustrated above in using published curves for some western pines, there is a clear need for a comprehensive study of the size-range method for each species pertinent to study in the Pacific Northwest (*i.e., P. albicaulis* Engelm., *P. contorta, P. monticola*, and *P. ponderosa*). Reasons for inclusion of *P. albicaulis* in this study are explained in the discussion section.

Possible distortion of *Pinus* pollen due to swelling in a given sedimentary environment (Praglowski, 1966) must remain conjectural for this study, since prior identification of the pollen types by morphological features is required to detect swelling, and the necessary diagnostic features presently are unknown for the genus. Another concern involving the size-range method, however, is one which could be tested easily—that of possible size variation of a species throughout its geographic range (Whitehead, 1964). Thus specimens of each species were obtained and measured for a number of localities spaced within its present geographic extent.

Methods

Samples used in this study came from three sources: fresh pollen collected in natural locations; fresh pollen collected from trees with a variety of origins, but all growing at the Institute of Forest Genetics, Placerville, California; and pollen removed from mature cones on herbarium sheets. All samples were prepared in the following manner: (1) acetolyze for five minutes (9:1 acetic anhydride: conc. sulfuric acid); (2) wash once with glacial acetic acid; (3) wash four times with distilled water; (4) after the third water wash samples were washed through a 125 μm mesh screen with 95 percent ethyl alcohol so as to allow all pollen through, while blocking most detritus; (5) wash once with 95 percent ethyl alcohol; (6) wash once with absolute ethyl alcohol; (7) wash once with benzene; (8) and mount in silicone oil (2000 centistokes viscosity). Opinion varies as to the effect of different types of chemical preparation (*e.g.,* KOH, acetolysis plus KOH, or acetolysis) on conifer pollen. Hansen (1947) did not acetolyze his samples, but treated them with KOH prior to examination; he reported significant swelling of pine pollen treated with KOH. Whitehead (1964) reported preliminary results on several species showing no such alteration. In a nonconifer pollen type, *Betula,* Faegri and Deuse (1960) found little swelling with KOH treatment, but noted more swelling with acetolysis. Since this issue is unresolved, I did not use KOH treatment. Acetolysis could not be avoided in this study, however, if accurate measurements were to be made of cleaned grains. Thus any error associated with this chemical preparation is inherent in the data presented here.

Glycerin jelly often is used to mount pollen grains for examination (Hansen, 1947; Ting, 1966), but a potential error in accurate size measurement work may exist when pollen is mounted in glycerin or glycerin jelly (Andersen, 1960). To avoid possible swelling of the grains, all samples were mounted in silicone oil. Departures from the procedure followed by Hansen (silicone oil versus glycerin jelly mounting and acetolysis

versus KOH treatment) were intended to test the size-range method under what are understood to be the most favorable conditions possible under laboratory procedures.

A Nikon (model SUBP) microscope with 100X objective and 10X Filar micrometer fitted ocular was used for all measurements, which were made to the nearest ocular line (1 line = 1 μm). Corpus breadth was considered to include the exine, in the manner followed by Hansen (personal communication). The dimension measured is illustrated in Figure 3. This subscribes to the definition of corpus breadth as depicted by Erdtman (1957). This dimension was measured for the first 100 fully expanded grains in the equatorial view encountered on sweeps across a slide of pollen from each geographic location. Width of these traverses across the slide was gauged so that no grain would be measured twice.

Results

Results of the corpus breadth study are summarized in Table 1, which lists by species the size range and mean, standard deviation, and locality of origin for all pollen samples studied. Data for each species display considerable range in the means from different localities, with all species having some pollen grains between 40 and 63 μm in breadth. *P. ponderosa* has the greatest range (32 to 72 μm), but limits of this range as well as those of other species studied may be in part a result of the sample size. Values obtained in this study appear comparable in their range and magnitude of those of Ting (1966), although he mounted his pollen in glycerin jelly.

Means and standard deviations of corpus breadth for *P. contorta* pollen samples collected at the Placerville arboretum are illustrated in Figure 4. These samples are considered separately in order to compare variation in pollen produced by trees of different origin, growing in the same locality. Considerable variation is evident in the corpus

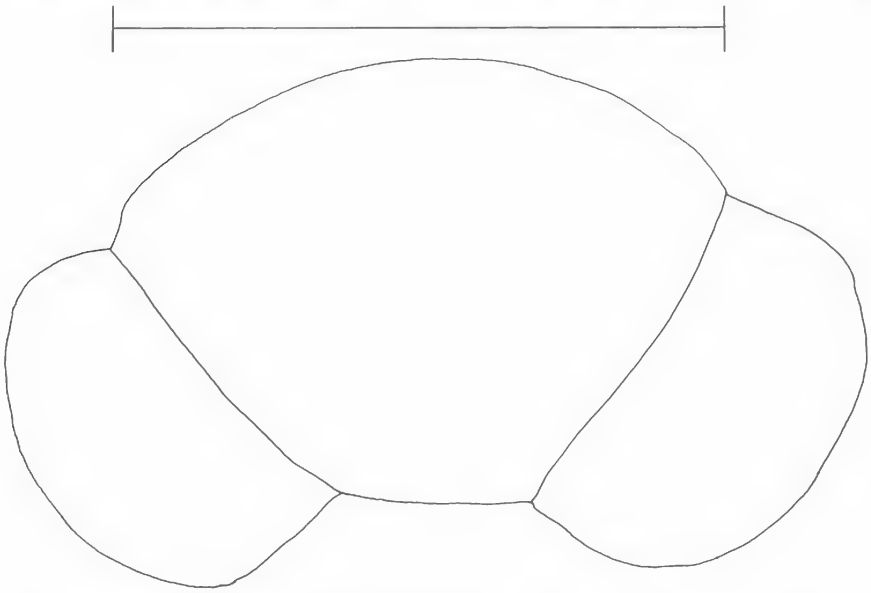

Figure 3. Illustration of pine pollen in equatorial view illustrating the dimension measured.

TABLE 1. Mean (micrometers), standard deviation, and range of variation of the corpus breadth of pollen from individual collections of four species of *Pinus* (100 measurements in each collection).

Species and locality	Mean size	Standard deviation	Size range
Pinus ponderosa			
Kettle Falls, Wash.	47.7	5.2	32-62
Colfax, Wash.	48.7	3.2	40-56
Harding Co., S.D.	49.4	2.7	42-55
Kamiak Butte, Wash.	51.5	4.4	39-61
Cliffdel, Wash.	52.4	3.8	42-65
Spokane Co., Wash.	53.3	3.6	44-65
Ronald, Wash.	54.1	4.9	40-72
Grand Coulee, Wash.	54.2	3.7	46-62
Almont, Colo.*	55.2	4.5	46-65
Pine Springs, Texas	55.2	3.8	45-67
Pend Oreille Co., Wash.	55.5	4.1	44-63
Stevens Co., Wash.*	56.3	4.4	45-66
Tieton Reservoir, Wash.	56.3	4.2	45-66
Chewelah, Wash.	56.5	3.3	46-63
Kamloops, Brit. Col.	56.8	3.2	49-65
Spokane Co., Wash.	57.7	4.3	48-72
Chinook Pass, Wash.	58.2	4.1	47-67
Fernie, Brit. Col.	58.5	3.4	45-66
Bear Lake, Wash.	61.1	4.5	53-70
Fort Spokane, Wash.	63.	3.7	53-72
Total population (n = 2000)	55.1	3.9	32-72
Pinus monticola			
Clearwater Co., Idaho	45.4	2.9	38-52
Naples, Idaho	49.6	2.8	42-56
Clarkia, Idaho	50.	2.7	43-58
Kaniksu N.F., Idaho	52.9	3.3	46-63
Shoshone Co., Idaho	53.1	3.9	41-62
Clearwater Co., Idaho	53.8	3.7	43-62
Clearwater Co., Idaho	53.8	4.2	44-66
Shoshone Co., Idaho*	54.7	3.7	48-67
Revelstoke, Brit. Col.	54.8	3.2	46-60
Clarkia, Idaho	57.	3.4	48-65
Shoshone Co., Idaho	57.	3.7	48-69
Clarkia, Idaho	57.1	3.6	47-66
Modoc Co., Calif.*	57.6	4.8	44-68
Total population (n = 1300)	53.5	3.6	38-69
Pinus contorta			
Bandon, Ore.**	41.3	5.1	32-46
Pend Oreille Co., Wash.	41.6	3.3	35-52
Bandon, Ore.**	43.6	2.	37-48
Mendocino Co., Calif.**†	44.8	1.9	41-50
Bandon, Ore.**	45.1	3.2	35-53
Cliffdel, Wash.	45.9	3.4	37-53
Kellers Ferry, Wash.	45.9	1.8	41-52
Victoria, Brit. Col.**	46.	2.6	40-53
Newport, Ore.**	46.	2.3	40-51
Reedsport, Ore.**	46.1	3.4	36-57
Kamloops, Brit. Col.	46.1	2.9	39-56
Yellowstone Park, Wyo.*	46.3	3.3	39-54
Cypress Hills, Alberta**	46.4	2.4	41-54

(continued).

TABLE 1. (continued).

Species and locality	Mean size	Standard deviation	Size range
Mt. Rainier Natl. Park, Wash.	46.7	2.8	39-58
Fernie, Brit. Col.	46.8	2.6	41-53
Auke Bay, Alaska	47.	2.5	42-54
Snoqualmie N.F., Wash.	47.1	2.8	39-56
Spokane Co., Wash.	47.1	3.7	39-57
Swauk Pass, Wash.	47.3	3.1	39-55
Rocky Mtn. Natl. Park, Colo.	48.	3.1	41-58
Noyo R., Calif.**	48.2	2.7	41-56
Okanogan, Wash.	48.2	2.8	42-58
Cody, Wyo.	48.3	3.5	41-60
Salmon La Sac, Wash.	48.3	3.1	43-56
Cody, Wyo.	48.4	3.3	38-55
Mendocino Co., Calif.**†	48.5	2.7	41-56
Idaho Co., Idaho*	48.5	3.4	42-56
Idaho City, Idaho	48.8	2.8	44-57
Vancouver Is., Brit. Col.**	48.5	4.3	41-56
Lane Co., Ore.*	49.2	2.8	44-56
Shuswap Lake, Brit. Col.**	49.5	3.1	43-56
Reedsport, Ore.**	49.9	3.	39-57
Cheekye, Brit. Col.*	49.9	2.4	44-56
Shoshone Co., Idaho*	49.9	3.4	44-58
Ochoco N.F., Ore.	50.2	3.2	44-63
Pendleton, Ore.	50.5	3.3	42-64
El Dorado Co., Calif.††	50.8	3.1	44-58
Fort Bragg, Calif.**†	50.9	2 7	43-56
Mt. Rainier Natl. Park, Wash.	51.4	3.6	42-62
Mt. Rainier Natl. Park, Wash.	51.6	3.2	43-58
Elmer City, Wash.	51.7	3.8	43-61
Idaho Co., Idaho*	51.8	3.	42-58
Salmon La Sac, Wash.	51.8	3.6	44-61
Crested Butte, Colo.*	51.8	3.6	44-62
Republic, Wash.	52.	3.6	44-61
Gunnison Co., Colo.	52.3	2.8	45-58
Pend Oreille Co., Wash.	52.5	4.	44-63
Yellowstone Park, Wyo.*	52.9	2.6	48-61
Friday Harbor, Wash.*	53.2	2.8	47-61
Long Lake Reserve, Brit. Col.**	53.3	2.8	45-59
El Dorado Co., Calif.††	56.1	3.1	48-62
Total population (n = 5100)	48.7	3.	32-64
Pinus albicaulis			
Mt. Adams, Wash.*	46.4	3.1	41-57
Superior, Mont.	49.4	4.7	39-62
Shoshone Co., Wash.*	51.1	3.2	44-58
Humboldt Co., Nev.*	52.2	3.8	43-62
Oakley, Idaho*	52.9	4.	46-64
St. Joe N.F., Idaho	54.3	3.9	43-63
Chelan Co., Wash.*	55.1	7.6	41-71
Pend Oreille Co., Wash.	58.6	5.1	47-69
Whatcom Co., Wash.*	59.	4.8	48-72
Idaho Co., Idaho*	60.3	4.	50-70
Grant Co., Oregon*	62.3	3.4	54-73
Total population (n = 1100)	54.7	4.9	39-73

** Sample from Placerville arboretum.

* Sample from herbarium material.

† *P. contorta* var. *bolanderi*

†† *P. contorta* var. *murrayana*

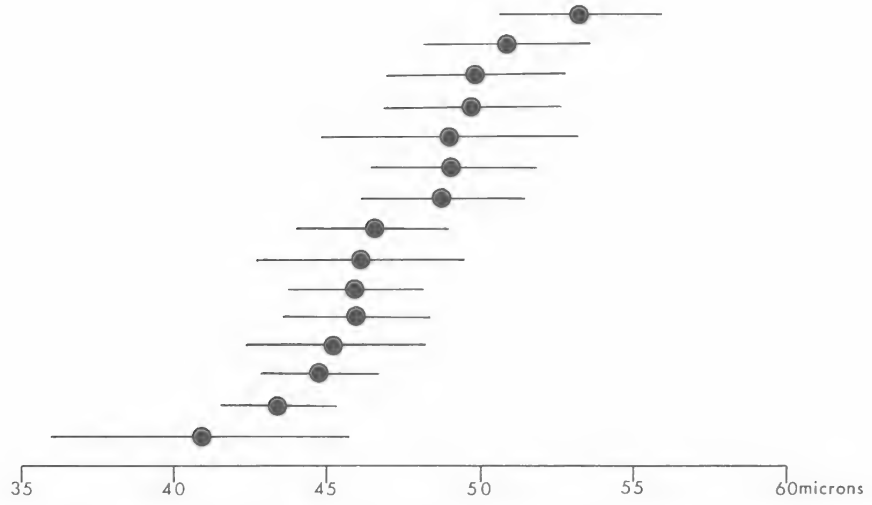

Figure 4. Variation in corpus breadth of individual samples of *P. contorta* from Placerville arboretum. Black dot represents mean, and horizontal line represents one standard deviation in either direction for 100 measurements per sample. Locality for each sample is given in Table 1.

breadth of this species, and thus at least some of the variation in corpus breadth displayed by *P. contorta* throughout its geographic range is genetically, rather than environmentally, controlled.

Included in the data for *P. albicaulis* is a sample from Chelan County, Wash., displaying marked variance ($\pm$ 7.5 μm). This sample contains a large number (approximately 50 percent) of aberrant grains with more than two bladders. In addition, some grains have only one bladder which completely encircles the corpus. This is a considerably higher percentage of aberrancy than Ting (1966) found as a regular occurrence among pollen of western pines. Measurements for this sample excluded abnormal pollen and were made of 100 grains having normal appearance. The sample is included in this study, since such pollen, in spite of its abnormalities, is part of the expectable pollen rain.

Neither pollen from arboretum trees nor samples collected from natural stands show corpus breadth to vary regularly with the geographic range for any of the four species. Detailed sampling of each population within the range of the species may or may not reveal a pollen-size cline in corpus breadth such as found for *Pinus echinata* Mill. (Cain and Cain, 1948).

Although not measured in this study, saccus breadth of *P. ponderosa* was observed frequently to be larger than those of the other pines. This agrees with Hansen's (1947) previous observation, but the comparatively larger size is not consistent within all samples in the present study.

Discussion

When the measurements for each species are compared to the size-range curves as constructed by Hansen (1947, Fig. 5), it is apparent that there is much more variation

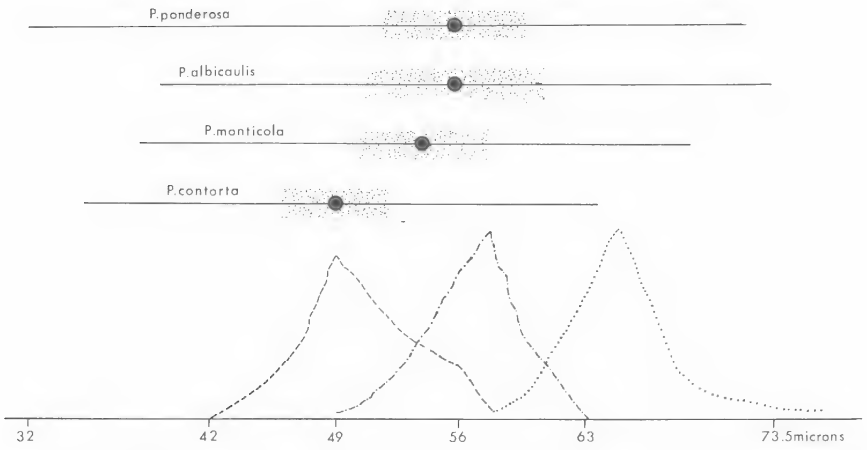

Figure 5. Corpus breadth variation in four pines (data from present study) as compared to Hansen's (1947) size-range curves. Illustrated variation does not include material from Placerville arboretum. The stippled area is one standard deviation on either side of the mean (the dot), and the horizontal line represents the range of variation.

in corpus breadth for all the species than had originally been assumed. Neither range nor standard deviation of corpus breadth can be used to separate one species' pollen from the other three. Range is a particularly weak statistic, since both upper and lower limits for any species' corpus breadth are established by the measurement of one pollen grain. Use of silicone oil in the present study, rather than glycerin jelly, as a mounting medium did not significantly improve the effectiveness of the size-range technique. Some error in measurement may have resulted from acetolysis (Faegri and Deuse, 1960) and the partial use of herbarium material in the study (Whitehead, 1964). These problems are probably minimal, considering the large variation in corpus breadth within each species compared to the potential size of these errors.

Hansen (1947) presents size frequency distributions of fossil pine pollen from several sites with bimodal and trimodal curves comparable to the curve peaks he found for modern pollen (Fig. 6). He noted also that the repeated occurrence of such distri-

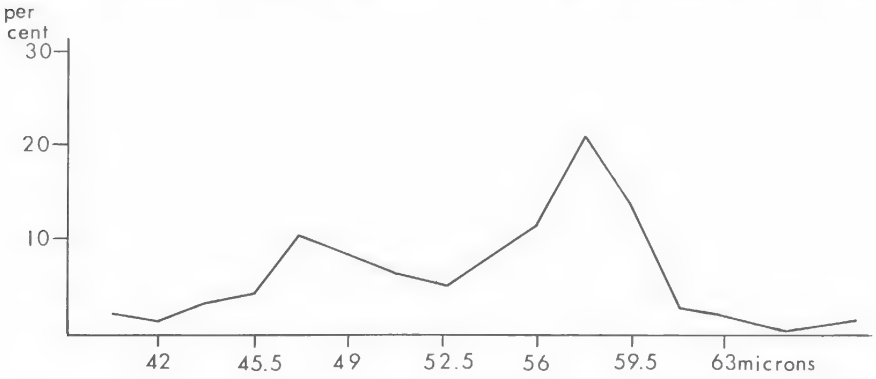

Figure 6. Size-frequency distribution of fossil pine pollen from a profile near Bonners Ferry, Idaho, constructed by Hansen (1947, Fig. 19).

butions in the fossil record appeared to substantiate the size-range method of identification. Distribution curves for the fossil record, however, unavoidably are constructed from measurements of unknown pollen, and consequently do not necessarily constitute solid support for the technique, even though curves of similar shapes are documented more than once. For example, considering difficulties encountered using size-range data in the present study, it becomes necessary to consider also some alternative explanations for these multipeaked curves. One such possibility is that contributing populations of the same species, each with the majority of its pollen of a different size than the others, might yield a curve having more than one peak. Substantial corpus breadth variation within the same species can occur in a small geographic area, as pollen examined in this study has demonstrated. Two samples of *P. ponderosa* pollen (Kettle Falls, Wash., and Fort Spokane, Wash., approximately 75 km apart) differ by 15μm in their means. If these two samples are considered as a 200-grain lot, measurements of their pollen grains could be plotted on axes of the same scale as used in Figure 6. The resultant size frequency distribution (Fig. 7) displays a general bimodal curve, yet

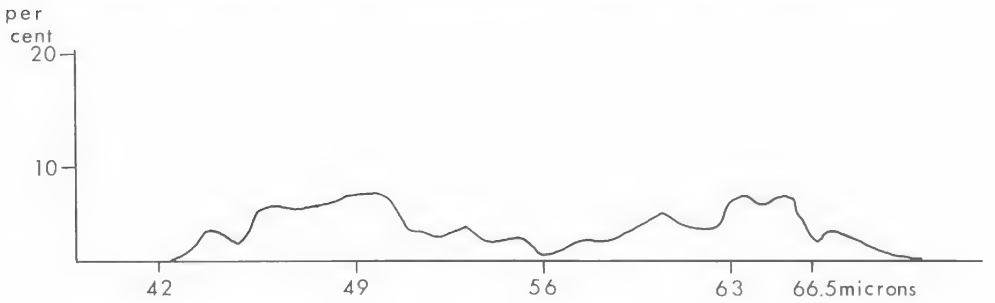

Figure 7. Size frequency distribution constructed by combining two samples of modern *P. ponderosa* pollen from the present study.

it was generated by pollen of only one species. Inexplicably, curves generated experimentally from data of the present study do not show the pronounced peaks displayed in many of Hansen's diagrams of fossil pollen. More detailed sampling may reveal that pollen size can vary substantially even within the same stand of trees, yielding an even greater variety of possible distributions with multiple peaks.

Certainly it is possible that multipeaked size frequency distributions of fossil pollen may be the product of several different pine species. Examples can be assembled from the present data of several species, growing in close proximity of each other, with pollen having measurably different sizes. Nevertheless, comparison of fossil distributions to modern pollen sizes for purposes of identification would be very difficult. One source of such difficulty is the environment of preservation of fossil pollen, which has an unpredictable effect on size. There are sufficient data available (Davis and Goodlett, 1960; Praglowski, 1966) to conclude that alteration of pollen does occur in a manner varying with sediment nature and pollen type. Adjustment for these indeterminable effects obviously is impossible at present, but it is clear that they further complicate the issue.

The size-range method also requires uniformity of pollen size for any species throughout its geographic range. Considering the movement of pine populations which

occurred in front of the retreating Cordilleran Ice Sheet, reforestation in areas formerly occupied by alpine glaciers, and possible ecotype extinctions, the pollen size for any extant population in a given locality is not necessarily equal to that dimension for a population which occurred there 12,000 years before. Of course, comprehensive information on size variation throughout the range of the extant populations does not determine the variation in fossil assemblages, but it does demonstrate the variability found within the species. This variability in corpus breadth is sufficient for the four species examined to hamper seriously the use of a size-range method for their identification.

Throughout his studies of fossil pollen collected at low elevation, Hansen did not include *P. albicaulis* pollen in the size-range curves used for identification, since he believed the pine was restricted to timberline (and consequently not near the bogs he examined) in postglacial time. Such elimination aided in distinguishing the other pines' pollen, for Hansen found *P. albicaulis* pollen to be intermediate in corpus breadth between *P. contorta* and *P. monticola.* Deevey (1948) questioned the elimination of *P. albicaulis* from consideration as a potential member of the postglacial vegetation, suggesting that altitudinal shifts in species were quite likely during postglacial time. Perhaps the present timberline habitat of this pine is similar to that in front of the ice during early postglacial time—certainly it is not so different as to cause the pine to be dismissed from attention. For this reason I examined *P. albicaulis* pollen, and found it to be quite variable in its corpus breadth. Such variability in this dimension makes impossible its identification by size range alone.

Hansen (1947), although apparently aware of some problems with using size range for species identification, felt it was better to separate the pines by this method than to consider them all collectively. Lumping all pine species' pollen in the pollen diagrams limits the basis for the interpretation of Quarternary vegetation. Considering the problems in using even his dimension standards derived from modern populations near the fossil localities, I disagree that the method's feasibility is supported by the consistency and logic of the pollen profile trends it produced as he maintained (Hansen, 1947). Such consistency may be an artifact of the small sample size of the modern pollen examined, the elimination of *P. monticola* pollen by severe overlap with other pollen types, the prior dismissal from consideration of *P. albicaulis* by an assumption, and the indeterminable amounts of all pine pollen assigned to the unidentified category.

The apparent low reliability of this technique becomes important in constructing vegetation history when large amounts of pine pollen are present in a region's record, and specific identifications based on corpus breadth are used to make major interpretations from this record. For example, in its present conception (Heusser, 1965, 1969) the post-Pinedale (P-2) vegetation chronology for eastern Washington consists of the following stages: I. *Pinus ponderosa* predominant 4000-0 years B.P.; II. Grasses, composites, and chenopods predominant 8000-4000 years B.P.; and III. *Pinus contorta* parkland 13,000-8000 years B.P. Throughout this sequence, which is based mainly on the work of Hansen, two pine species (*P. contorta* and *P. ponderosa*) play major roles. Apparently the basis for these interpretations rests on the size-range technique. Results of the present study indicate this is a tenuous base from which to make such widespread interpretations. This size-range method is not sufficiently accurate to make specific determinations of pollen among the pines in question. As a result our concepts of postglacial vegetation in this region may require reevaluation or at least substantiation by different lines of evidence.

In the current absence of a reliable identification technique based on pollen morphology the best substitute appears to be use of pine macrofossils in situ with the pollen (Baker, 1970). Errors inherent in use of macrofossils (*e.g.,* bias of preservation and generally short transport) limit its usefulness. Hopefully some new technique (*e.g.,* scanning electron microscopy) will reveal persistent, ubiquitous, morphologic differences among various pine species' pollen as a final solution to the identification dilemma.

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Literature Cited

Andersen, S. T. 1960. Silicone oil as a mounting medium for pollen grains. Danm. Geol. Unders. IV Raekke BD. 4 NR. 1.

Baker, R. G. 1970. Pollen sequence from Late Quaternary sediments in Yellowstone Park. Sci. 168: 1449-1450.

Bright, R. C. 1966. Pollen and seed stratigraphy of Swan Lake, southeastern Idaho; its relation to regional vegetational history and to Lake Bonneville history. Tebiwa 9: 1-47.

Cain, S. A. 1940. The identification of species in fossil pollen of *Pinus* by size frequency determination. Am. J. Bot. 27: 301-308.

Cain, S. A., and L. G. Cain. 1944. Size frequency studies of *Pinus palustris* pollen. Ecology 25: 229-232.

————., and ————. 1948. Size frequency characteristics of *Pinus echinata* pollen. Bot. Gaz. 110: 325-330.

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Expt. Sta. Tech. Bull. 60.

Davis, M. B., and J. C. Goodlett. 1960. Comparison of the present vegetation with pollen-spectra in surface samples from Brownington Pond, Vermont. Ecology 41: 346-357.

Deevey, E. S., Jr. 1948. Review of Hansen (1947). Geog. Rev. 38: 345-347.

Erdtman, G. 1957. Pollen and Spore Morphology. Plant Taxonomy II. Stockholm.

Faegri, K., and P. Deuse. 1960. Size variations in pollen grains with different treatments. Pollen et Spores 2: 293-298.

Franklin, J. F., and C. T. Dyrness. 1969. Vegetation of Oregon and Washington. U.S.D.A. Forest Serv. Res. Pap. PNW-80.

Hansen, H. P. 1940. Paleoecology of a montane peat deposit at Bonaparte Lake, Washington. Northwest Sci. 14: 60-69.

————. 1947. Postglacial forest succession, climate, and chronology in the Pacific Northwest. Trans. Am. Phil. Soc. 37: 1-130.

Heusser, C. J. 1960. Late-Pleistocene environments of North Pacific North America. Am. Geog. Soc. Spec. Publ. No. 35.

————. 1965. A Pleistocene phytogeographical sketch of the Pacific Northwest and Alaska. The Quaternary of the United States (ed. by H. E. Wright, Jr. and D. G. Frey), 469-483. Princeton.

————. 1969. Late-Pleistocene coniferous forests of the northern Rocky Mountains. Coniferous Forests of the Northern Rocky Mountains (ed. by R. D. Taber), 1-23. Missoula.

Praglowski, J. 1966. On pollen size variations and the occurrence of *Betula nana* in different layers of a bog. Grana Palynol. 6: 528-543.

Schultz, C. B., and H. T. U. Smith. 1965. Guidebook for Field Conference J (Pacific Northwest) INQUA. Lincoln.

Ting, W. S. 1960. Determination of *Pinus* species by pollen statistics. U. C. Publ. in Geol. Sci. 58.

Whitehead, D. R. 1964. Fossil pine pollen and full-glacial vegetation in southeastern North Carolina. Ecology 45: 767-777.

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Bacteria in the Wood of Living Aspen, Pine, and Alder[2]

Introduction

The investigations on the microflora in the wood of living trees have up to now dealt almost entirely with the microorganisms associated with diseased trees. However, D. M. Knutson and E. Sucoff (in press) in 1968 reported large numbers of bacteria in the aseptically expressed sap of trembling aspen, *Populus tremuloides,* and Etheridge (1961) observed bacteria in the branches and stems of aspen. Basham and Taylor (1965) found fungi and bacteria in normal and discolored heartwood of second growth sugar maple in Ontario. Bacterial attack and deterioration of pine logs in pond storage had been described by Ellwood and Ecklund (1959) and Knuth and McCoy (1962). Lutman and Wheeler (1948) and Samisa and Etinger-Tulczyuska (1963) reported on the distribution of bacteria in tissues of healthy potatoes and tomatoes.

The present investigation consisted primarily of a study of the bacteria occurring in non-distressed wood of living trees, *Populus tremuloides* Michx., *Pinus ponderosa* Dougl. ex. Lawson, and *Alnus tenuifolia* Nutt. Aspen was chosen for the project because some research had already been done on the microflora contained in its wood. The other tree species were chosen because of their availability and occurrence in the same habitat with aspen.

The investigators were especially concerned with determining what species of bacteria occur in wood; the known habitats or sources of original isolation of these species as recorded in the literature might be a key to the discovery of the processes by which wood bacteria are introduced into trees.

The present project was regarded as a preliminary work with many possible informative and useful ramifications. Therefore, the investigators were also interested as to whether the species of bacteria that were isolated belong to genera known or suspected to include plant pathogens or decomposers of materials from dead or dying trees. Since Knutson and Sucoff reported that isolates of *Bacillus* and *Erwinia* from wood grew on Ashby's nitrogen-free medium the isolates in the present study were tested on the same kind of medium.

Methods and Materials

Location and description of the collection area. Wood samples were collected from an area located 2.9 miles from Cheney, Spokane County, Washington. The altitude

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here is approximately 2300 ft. (700 mi). The average yearly temperature is about 48°F (9°C) and the average monthly rainfall is 1.54 in. (3.9 cm). The collection area is mostly of basaltic scabrock formation. It is moderately forested with ponderosa pine, and has occasional stands of aspen and alder associated with a small eutrophic pond.

Field collection techniques. Cylinders of wood were secured from the trunks of living trees in the field by removing a portion of bark and cambium, approximately six mm square, and quickly inserting an increment borer. The bark and cambium were removed to decrease the possibility of contamination from the air and exposed surfaces. The hole in the tree from which the sample was taken was stoppered with a piece of fitted wood which had been presterilized in a 10 percent hypochlorite solution. The site of cylinder removal was approximately 1.2 m from the ground, a distance chosen empirically. Upon removal, the sample cylinder was transferred immediately to a sterile petri dish, which was placed in a polyethylene bag to lessen changes in moisture content, and stored at -5°C until assayed. The diameter of the sample boring was four mm and the average diameter of the trees sampled was approximately 15 cm. The length of the sample cylinder represented the radius of the tree sampled, from the cambium to the pith cylinder. Only samples containing apparently nondiseased wood were selected for testing.

Laboratory procedures. The work room where all grinding and transfers were carried out was first steamed and the working area was thoroughly washed with a 10 percent hypochlorite solution. The sample boring was surface-sterilized by washing in a solution of 10 percent hypochlorite for four minutes. This specific amount of time was selected through experiments with wooden cylinders coated with cultures of *Bacillus* sp. and manured soil. After sterilization, the boring was given three, two-minute rinses in presterilized water contained in petri dishes. A control to check the efficiency of the sterilization procedure was attained by pouring sterile melted double-strength trypticase soy agar (BBL) into the rinse water plates and incubating this agar-rinse water mixture.

With sterile forceps, the sample boring was then transferred to a sterile Waring Commercial Blendor (Eberbach Corporation) with 150 ml of sterile water and ground for four minutes at low speed to attain the degree of fragmentation considered necessary for practical optimum yield of microbial colonies. Petri dishes with approximately 20 ml of agar were inoculated with 0.5 ml of fragmented wood suspension. The inoculum was positioned near the edge of the plate with a sterile pipet and then streaked with a sterile inoculating loop to obtain isolated bacterial colonies.

Three types of agar plates were used for the preliminary isolation of organisms. Eosin methylene blue agar, EMB agar (BBL), was used for the isolation and differentiation of gram-negative bacilli; trypticase soy agar, TSA (BBL), was used as a general-purpose medium for the growth of most aerobic bacteria; malt agar (Difco) was used for the isolation of yeasts and mycelial fungi. Kligler's iron agar (Difco) was used in an attempt to isolate hydrogen sulfide-forming anaerobic bacteria. Tubes of this medium were inoculated with fragmented wood suspension, and incubated in a GASPAK anaerobic jar (BBL) at 30°C. Duplicate culture plates from each sample were incubated, one at 30°C and one at 14°C. The 14°C incubation temperature was employed to promote growth of psychrophilic bacteria.

After 72 hours of incubation, plates were observed to determine the number and types of colonies present. The cultures were examined at regular intervals after 72 hours to check for new colony growth. Plates were not discarded until after at least seven days of incubation. Colonies were observed for difference in color, size, texture, and gram-staining properties of the cells. The colonies were examined with the aid of a Quebec colony counter although no definitive quantitative study was attempted here. An inoculum from each type of bacterial colony on a given plate was transferred to a tube of TSA; fungi were transferred to Sabouraud's dextrose agar (Difco). Isolates were maintained at room temperature.

All of the bacterial isolates were tested for the following properties using the media listed: Fermentation with production of acid or acid and gas of glucose, maltose, lactose, sucrose and mannitol: phenol red broth (Difco). Gelatin digestion: nutrient gelatin (Difco). Citrate utilization: Simmon's citrate medium (Difco). Urease production: urea broth (Difco). Ammonia production: peptone broth (Difco). Motility: motility medium (BBL). Indol production: tryptone broth (Difco). Hydrogen sulfide production: Kligler's iron agar (BBL). Acetyl methyl carbinol production: methyl-red-Voges-Proskauer medium (Difco). Determinations of the bacterial isolates were made by referring to *Bergey's Manual of Determinative Bacteriology.*

Tests were also conducted on the isolates for starch digestion using 1 percent soluble starch in nutrient agar (Difco); pectin digestion using a pectate medium described by Hungate and Fletcher (1961); cellulose utilization using a variant of a medium described by Hungate (1957); and for growth on Ashby's nitrogen-free medium.

Results

Microorganisms isolated. The bacterial species isolated were identified as follows: *Achromobacter parvulus* (Conn, 1922) Breed, 1953, five isolates; *Arthrobacter ureafaciens* (Krebs and Eggleston, 1939) Clark, 1955, three isolates; *Brevibacterium ammoniagenes* (Cooke and Keith, 1927) Breed, 1953, five isolates; *Brevibacterium insectiphilium* (Steinhaus, 1941) Breed, 1953, four isolates; *Brevibacterium linens* (Weigmann, 1910) Breed, 1953, seven isolates; *Cellulomonas acidula* (Kellerman *et al.,* 1913) Bergey *et al.,* 1923, one isolate; *Corynebacterium humiferum,* Seliskar, 1952, six isolates; *Erwinia amylovora* (Burrill, 1882) Winslow *et al.,* 1920; four isolates; *Erwinia salicis* (Day, 1924) Chester, 1939, one isolate.

Sources of the isolates. The numbers and sources of wood samples positive for each of these species are shown in Table 1. Although no definitive study for the quantitative distribution of bacteria was carried out here, the wood of aspen appeared to contain more bacteria than that of the pine or alder. All nine of the identified species of bacteria were found to occur in aspen.

Isolation temperatures. Of the two incubation temperatures used, 30°C and 14°C, that of 30°C was the better for obtaining good growth, and no species were isolated by culturing at 14°C which were not also obtained under mesophilic conditions. No bacterial isolations were obtained through the anaerobic culture procedures.

Tests with gelatin, pectate, cellulose, nitrogen-free and starch media. Table 2 shows the results of the tests for gelatin digestion, pectin digestion, cellulose utilization, and growth on a nitrogen-free medium. All of the isolates tested negative for starch hydrolysis.

TABLE 1. Sources of bacterial isolates. Numbers of samples from each tree species which were positive for bacteria.

Bacterial isolates	Aspen[a]	Pine[b]	Alder[c]
Achromobacter parvulus	2	3	1
Arthrobacter ureafaciens	3		
Brevibacterium ammoniagenes	3		2
B. insectiphilium	4		
B. linens	1	5	1
Cellulomonas acidula	1		
Corynebacterium humiferum	4		2
Erwinia amylovora	1	3	
E. salicis	1		

[a] Number of samples—52.
[b] Number of samples—41.
[c] Number of samples—29.

TABLE 2. Results of testing bacterial isolates from wood with nutrient gelatin, pectate, cellulose, and nitrogen-free media.

Bacterial isolates	No. of strains tested	Gelatin digestion	Growth on Ashby's nitrogen-free medium	Cellulose utilization	Pectin digestion
Achrombacter parvulus	5	+	+	−	−
Arthrobacter ureafaciens	3	+	−	−	+
Brevibacterium ammoniagenes	5	−	+	−	−
Brevibacterium insectiphilium	4	+	−	−	−
Brevibacterium linens	7	+	−	−	+
Cellulomonas acidula	1	+	+	+	+
Corynebacterium humiferum	6	−	+	−	+
Erwinia amylovora	4	+	+	−	−
Erwinia salicis	1	−	+	−	+

Fungi isolated. Mycelial fungi were isolated from all three tree species. The wood samples tested for fungi were identical with those tested for bacteria. Fourteen isolates were made including four different types of fungi.

A phycomycete, probably in the order Mucorales, was isolated from all three tree species. It was found to be a pectin digester, but had no effect on cellulose. An ascomycete resembling the genus *Penicillium* was isolated from aspen and alder. In addition to these, two unidentified types of fungi with white mycelia were isolated from aspen.

Two yeast isolates were made from aspen. Colonies of both were white to cream in color, both had small oval cells which reproduced by budding. Neither of these isolates was identified further.

Discussion

As it has been established that bacteria may be present in the wood of living trees, one of the first questions to arise involves their mode of entry. The original sites of isolation and/or habitats of the bacterial species isolated in the present study had been reported as follows: *Achromobacter parvulus*—isolated from manure and found generally in the soil (Breed *et al.,* 1957). *Arthrobacter ureafaciens*—widely distributed in nature. Isolated from frozen foods (Komagata and Ogawa, 1966). *Brevibacterium ammoniagenes*—isolated from feces of infants and known to be associated with diaper rash of infants. Widely distributed in nature and found extensively in putrefying material (Breed *et al.,* 1957). *B. insectiphilium*—isolated from the body wall of bagworm, *Thyridopteryx ephemaeriformis* Haw. Habitat unknown (Breed *et al.,* 1957). *B. linens*—found in dairy products, in various grains, silage, green plants, water pools, manure, soil and air (Breed *et al.,* 1957). Has been isolated from frozen foods (Komagata and Ogawa, 1966). *Cellulomonas acidula*—isolated from soil in Utah (Breed *et al.,* 1957). *Corynebacterium humiferum*—previously isolated from *Populus tremuloides* and reported to be pathogenic to the Lombardy popular, *Populus nigra* var. *italica* (Breed *et al.,* 1957). *Erwinia amylovora,* isolated from blossoms and leaves of pear and apple trees. Reported to attack a large number of species in several tribes of the family Rosaceae (Elliot, 1951). *E. salicis,* isolated from the cricket-bat willow, *Salix caerula,* and from the white willow, *S. alba.* Reported to cause a water-mark disease of willow in England (Dowson, 1957).

Therefore, all of these bacterial species except *Brevibacterium insectiphilium, Erwinia amylovora,* and *E. salicis* may be regarded as primarily soil bacteria or of such diverse distribution that they may be assumed to occur in soil. This suggests the possibility that the presence of these in wood may be due to transport from the soil by way of the tree roots. This entrance might be facilitated by mechanical injury to the roots through burrowing insects, nematodes, and other small animals inhabiting the soil. Possibly the bacteria may also enter the wood through wounds in the leaves and stems made by aphids and other insects.

Possibly the bacteria in wood of nondiseased trees are reproducing at a very low rate or not at all, but are kept viable because the tree sap prevents their desiccation and may provide minimal nutrition. But, in itself, their presence in the wood suggests their possible significance in the ecology of diseased, nondiseased, and dead plant materials and the soil-plant association which should warrant extensive and diverse future investigations.

Five of the species of bacteria from the present study were shown to be pectin digesters and one, *Cellulomonas acidula,* utilized cellulose (Table 2); six species showed proteolysis. These properties may indicate potentials for invasion of plant cells.

It has been suggested that if digesters of pectin and cellulose found in soil and water gain entrance into wood they may cause a reduction in its strength. According to Haygreen and Wang (1966), bacteria could be the cause of reduced strength in aspen wetwood, assuming that wood is a suitable growth substrate. Bacteria in aspen lumber have been studied by Clausen, Rees, and Kaufert (1949) in relation to wood collapse. *Bacillus polymyxa* (Prazmowski) is a strong digester of pectin and cellulose, but, although Knuth and McCoy (1962) found this species occurring in pine logs in pond storage, their study produced no evidence that it reduced wood strength.

The presence in wood of microorganisms which digest pectin and cellulose also suggests that wood from freshly cut trees or branches may contain the agents of its own decomposition. It was the hypothesis of Springer and Hajny (1966) that release of heat in wood chip piles sometimes to the point of ignition might be due to oxidation of various wood constituents by microorganisms. But they found that the bacterial population in wood chips was very low, not high enough to cause sufficient oxidation for ignition. This assumption, however, does not preclude the possibility that microorganisms already present in wood can be important in its eventual decomposition. The small numbers of bacteria in sawdust reported by Springer and Hajny could be due to the drying out of the wood before sawing as bacterial cells in the vegetative stage seldom withstand slow desiccation.

Six of the bacterial species studied grew on a nitrogen-free medium (Table 2). However, growth on Ashby's medium is by itself not a sufficient proof that a bacterium fixes nitrogen, and further tests with the isolates are in order.

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Literature Cited

Basham, J. T., and L. D. Taylor. 1965. The occurrence of fungi and bacteria in normal and discolored heartwood of second growth sugar maple in Ontario. Plant Disease Reporter. 49: 771-774.

Breed, R. S., E. G. D. Murray, and N. R. Smith. 1957. Bergey's Manual of Determinative Bacteriology, 7th ed. Williams and Wilkins Co., Baltimore.

Clausen, V. H., L. H. Rees, and F. H. Kaufert. 1949. Development of collapse in aspen lumber. Forest Prod. Res. Soc. Proc. 3: 460-468.

Dowson, W. J. 1957. Plant Diseases Due to Bacteria. Cambridge University Press, London.

Elliot, C. 1951. Manual of Bacterial Plant Pathogens. Chronica Botanica., Waltham, Mass.

Ellwood, E. L., and B. A. Ecklund. 1959. Bacterial attack on pine logs in pond storage. Forest Prod. J. 9: 283.

Etheridge, D. E. 1961. Factors affecting branch infection in aspen. Can. J. Bot. 30: 799-816.

Haygreen, J. G., and S. S. Wang. 1966. Some mechanical properties of aspen wetwood. Forest Prod. J. 16: 118-119.

Hungate, R. E. 1957. Laboratory Manual of General Bacteriology, 1st ed. Scholar's Library, New York.

———— and D. W. Fletcher. 1961. Laboratory Manual of General Bacteriology, 2nd ed. Scholar's Library, New York.

Knuth, D. T., and E. McCoy. 1962. Bacterial deterioration of pine logs in pond storage. Forest Prod. J. 12: 437-442.

Komagata, K., and H. Ogawa. 1966. Microbiological studies of frozen foods: Determination of gram-positive bacteria isolated from frozen food. Shokuhin Eiseigaker Zashi. 7: 248-259.

Lutman, B. F., and H. E. Wheeler. 1948. *Bacillus megaterium* de Bary from the interior of healthy potato tubers. J. Washington Acad. Sc. 38: 336-340.

Samisa, Z., and R. Etinger-Tulczyuska. 1963. Distribution of bacteria within the tissue of healthy tomatoes. Appl. Microbiol. 11: 7-10.

Springer, E. L., and G. J. Hajny. 1966. Spontaneous heating in piled wood chips. TAPPI 53: 85-86.

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Biostratigraphy of the Marine Eocene near Seattle, Washington

Introduction

The fossils of the marine Eocene basaltic wacke south of Seattle, Washington (Fig. 1) were studied by White (1888, 1889) who correlated them with those of the Tejon of California and cited the opinion of Bailey Willis that these rocks were no older than the Puget Group. Weaver (1937) mapped these rocks and concluded "they are interstratified with continental beds of the Puget Group and are definitely of upper Eocene age and represent a time equivalent to that of the Tejon formation of southern California." Durham (1942) described three new fossil coral species from these strata and noted that one was hermatypic and thus suggestive of subtropical climate in this area during the upper Eocene. Waldron (1962) and Waldron *et al.* (1962) mapped the basaltic wacke as "middle Eocene sedimentary rocks" underlying the Tukwilla Formation (Figs. 2 and 3). I disagree with Waldron's interpretation and believe the interpretation of the earlier workers is correct.

Stratigraphic Relations

My interpretation is based in part on my mapping of the area (Fig. 1), which shows that the marine basaltic wacke is interstratified with rocks typical of the Tukwilla Formation of the type area. For example, the arkosic wacke in Figure 1 is a tan-weathering, light gray, medium-grained wacke interbedded with light gray siltstone and contains abundant fossil plant fragments, especially *Equisetum.* These rocks are lithically identical to rocks of the Tukwilla Formation, exposed in the type area one and a half miles to the southeast, which also contains abundant *Equisetum* and other plant fragments (sections 11 and 14, Fig. 3). This portion of the type Tukwilla was mapped as "poorly cemented arkosic sandstone" by Waldron *et al.* (1962) and as the middle member of the Tukwilla Formation by Mullineaux (1970). The andesite conglomerate in Figure 1 is a rusty-weathering, gray andesite cobble conglomerate and breccia. These rocks closely resemble the andesite flows, conglomerate, and breccia widely exposed in the type area. Waldron *et al.* (1962) mapped this part of the type Tukwilla as "sandstone, conglomerate and breccia that consist of volcanic rock fragments." Mullineaux (1970) mapped these same rocks in the type area as the upper and lower members of the Tukwilla Formation. The tan-weathering, dark greenish-gray basaltic wacke shown in Figure 1 locally contains abundant marine fossils but is not known in the type area of the Tukwilla. My cross section A-B, based on my map in Figure 1, shows the interstratification of the basaltic wacke with arkosic wacke and andesite conglomerate, both of which are identical to that found in the type area of the Tukwilla. In summary, this evidence of interstratification strongly supports my argument that the marine basaltic wacke is a part of the Tukwilla Formation.

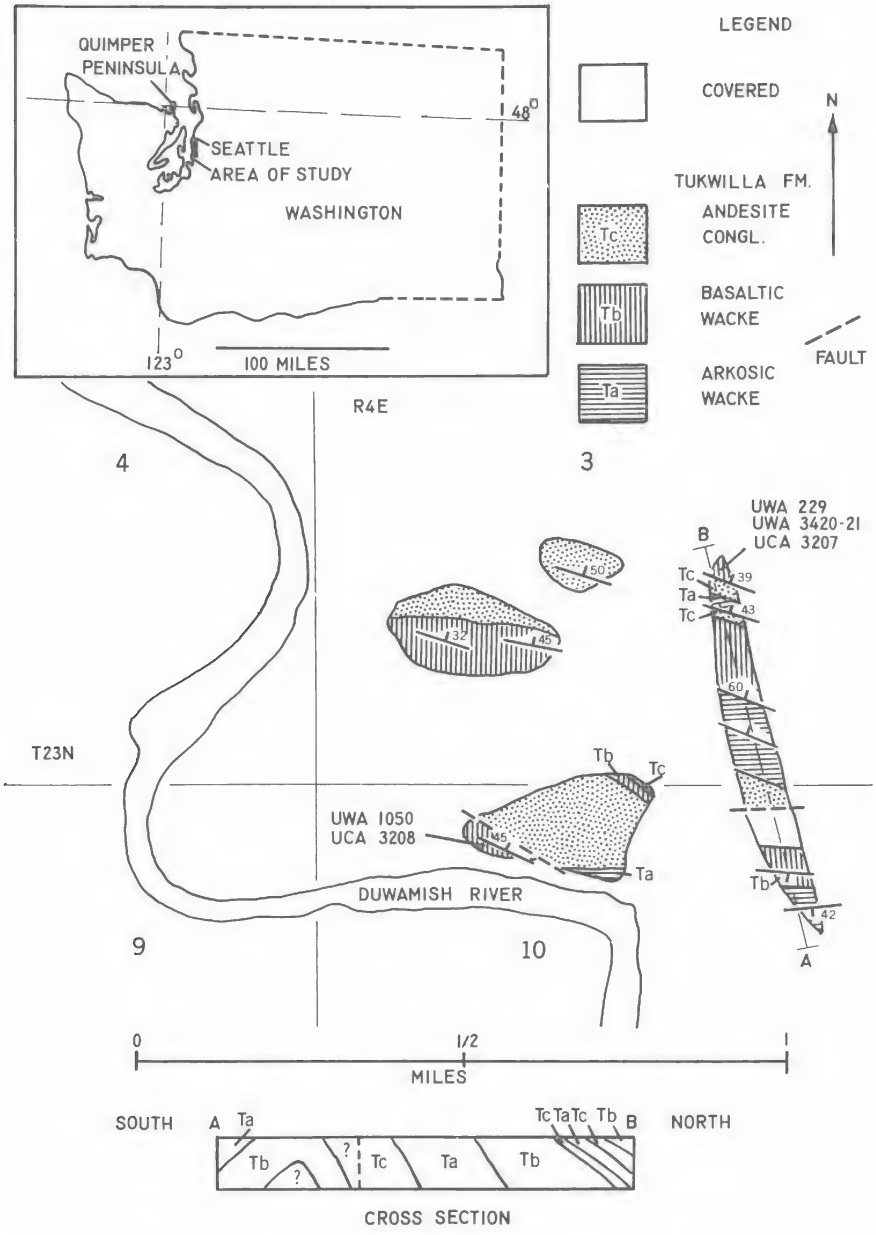


Figure 1. Geologic map and cross section of the area south of Seattle, Washington. Fossil localities are designated by numbers prefixed by UWA and UCA.

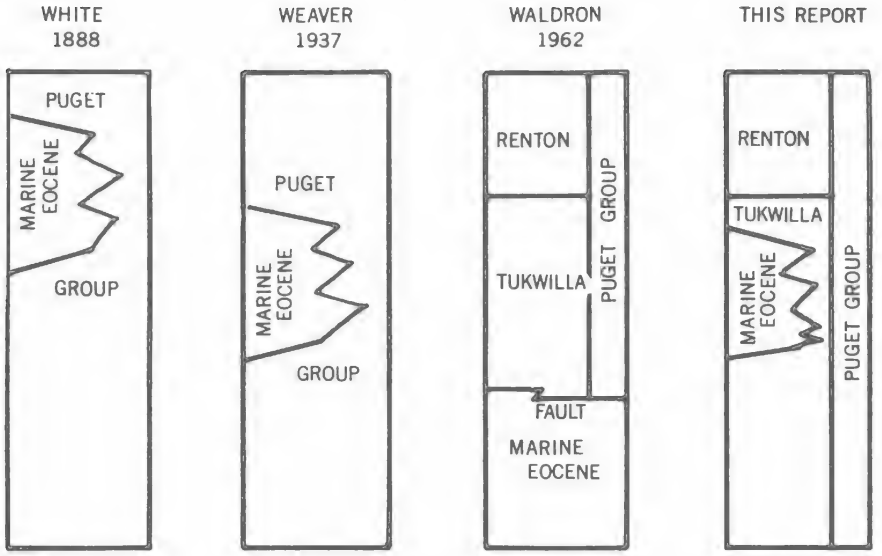


Figure 2. Different authors' interpretation of the stratigraphic position of the marine Eocene rocks near Seattle.

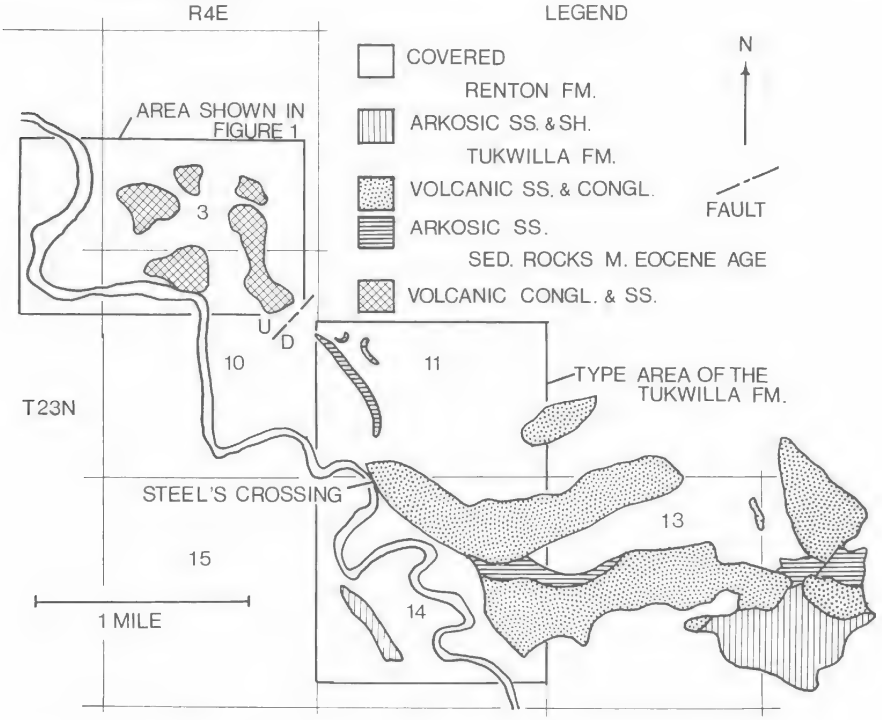


Figure 3. Geologic map of the type area of the Tukwilla formation and the area shown in Figure 1. After Waldron *et al.* 1962.

Paleontologic Evidence

The fossils from the basaltic wacke indicate an upper Eocene rather than middle Eocene age for these rocks. Of the 48 species collected (Table 1), nine are restricted to the upper Eocene Narizian Stage (Mallory, 1959) and one has previously been recorded only from the Eo-Oligocene Refugian Stage (Schenck and Kleinpell, 1936). None, however, is restricted to the middle Eocene (Table 2).

Wolfe (1968) assigned three localities definitely known to be within the Tukwilla Formation to the Ravenian Stage which he defined on fossil plants. He regarded the Ravenian Stage to be correlative of the Transition through Tejon marine megafossil "stages" of Weaver *et al.* (1944). However, there are only two places where Ravenian Stage plants are found with rocks of known age (Wolfe). One is the occurrence of upper Ravenian plants in the McIntosh Formation which is known to be of Narizian age (Tejon "stage" of Weaver *et al.,* 1944). The other is the occurrence of upper Ravenian plants in the basal Fisher Formation of probable Refugian age (Keasey "stage" of Weaver *et al.,* 1944). These correlations are in agreement with my assignment of the marine Tukwilla Formation to the upper Eocene Narizian Stage noted previously and further support my inclusion of these rocks in the Tukwilla Formation.

Correlation

The basaltic wacke of the Tukwilla is lithically identical to and contains many of the same fossils as does the lower Lyre Formation in the Quimper Peninsula area (Table 2). This part of the Lyre was regarded as of upper Eocene age by Weaver (1937) and Durham (1944). Allison (1959) and Thoms (1959) described in detail the geology of the Quimper Peninsula area in unpublished University of Washington masters theses. Allison reported 12 species of megafossils from the lower Lyre which are restricted to the upper Eocene and above. He also noted five species previously recorded only from the middle Eocene. However, all of the positively identified foraminifers reported by Thoms from these rocks have been previously recorded from the Narizian and five species are restricted to that stage.

The basaltic wacke of the Tukwilla Formation also contains fossils characteristic of the Cowlitz Formation of southwestern Washington (Table 2).

Paleocology

The fossils of the basaltic wacke are concentrated in thin layers with thick barren layers between. These appear to be current concentrated shell beds. This is suggested by the stratification of elongate taxa such as *Dentalium, Turritella, Ficopsis, Conus,* and *Exilia* parallel to the bedding. The effect of current is also suggested by the separation of nearly all pelecypod valves; especially *Microcallista,* the most abundant clam. There is evidence of abrasion on nearly all specimens.

Specimens larger than 15 mm are scarce, although the taxa represented are commonly larger elsewhere in the Eocene of the Northwest. This may be due to size-sorting by currents. The specimens of *Microcallista,* for example, show a normal (bell-shaped) size-frequency distribution and most are between 5-10 mm in length. Fagerstrom (1964) argued that a normal size-frequency distribution indicates winnowing or transportation of the assemblage by currents. Hallam (1967), on the other hand, concluded that the normal size frequency distribution may be the result

CHECK LIST OF FOSSILS FROM THE MARINE EOCENE NEAR SEATTLE, WASHINGTON

TABLE 1

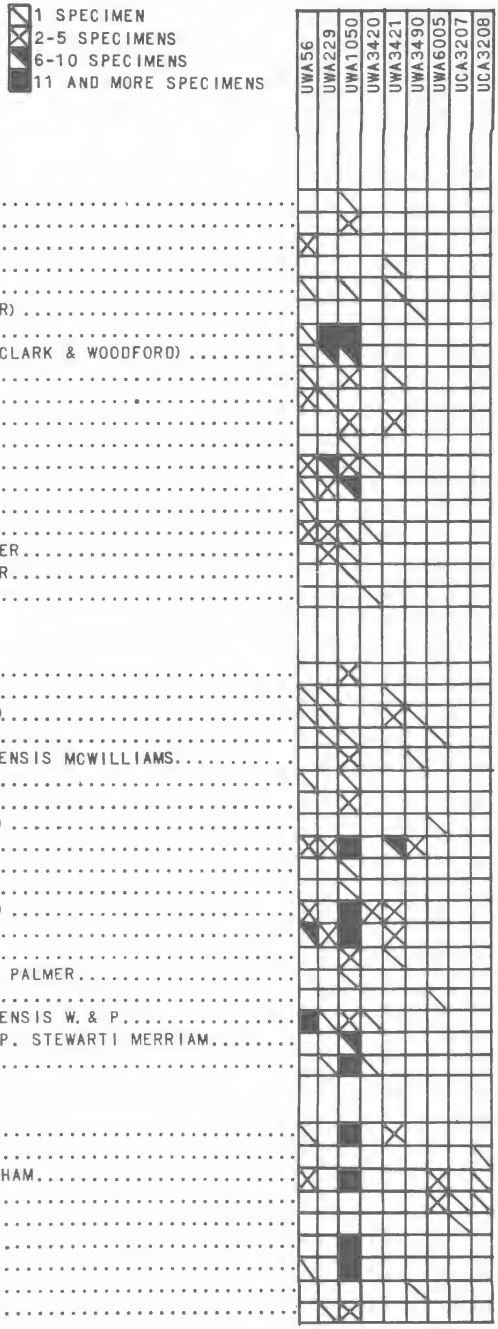
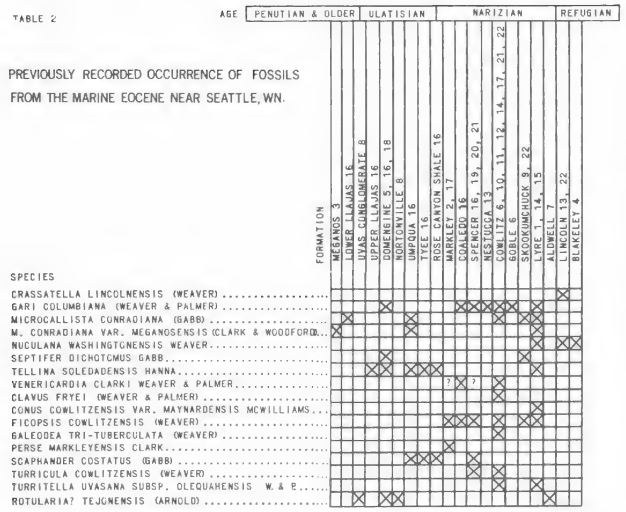


TABLE 1. Check list of fossils from the marine Eocene near Seattle, Washington.

TABLE 2

PREVIOUSLY RECORDED OCCURRENCE OF FOSSILS FROM THE MARINE EOCENE NEAR SEATTLE, WN.



REFERENCES

1 ALLISON, R.C., 1959
2 CLARK, B.L., 1936
3 CLARK, B.L. & WOODFORD, A.O., 1927
4 DURHAM, J.W., 1944
5 KEEN, A.M. & BENTSON, H., 1944
6 LIVINGSTON, V.E., 1966
7 MCWILLIAMS, R.G., 1965 (B)
8 MALLORY, V.S., 1959
9 PEASE, M.H. & HOOVER, L., 1957
10 ROBERTS, A.E., 1958
11 SCHENCK, H.G., 1926
12 STEWART, R.B., 1930
13 SNAVELY, P.D. & VOKES, H.E., 1949
14 TEGLAND, N.M., 1931
15 THOMS, R.E., 1959
16 TURNER, F.E., 1938
17 VERASTEGUI, P., 1953
18 VOKES, H.E., 1939
19 VOKES, H.E., ET AL., 1951
20 VOKES, H.E., ET AL., 1954
21 WARREN, W.C., ET AL., 1945
22 WEAVER, C.E., 1942

TABLE 2. Previously recorded occurrence of fossils from the marine Eocene near Seattle, Washington.

of factors other than transportation by currents. I conclude that because of the evidence for transportation previously noted, currents have sorted and moved this assemblage to its present site and this explains the scarcity of large fossils.

The fossils are suggestive of shallow water because of the occurrence of *Conus, Sinum, Gari, Ostrea,* and *Septifer*, all of which are reported only from depths less than 25 fathoms on the Pacific coast (Keen, 1963). In addition, *Acmacea, Calyptraea, Turritella, Crassatella, Olivella, Solen,* and *Tellina* are all reported only from depths less than 100 fathoms (Keen, 1963). Their occurrence with the hermatypic coral, *Astreopora,* is also suggestive of depths less than 45 fathoms (Durham, 1947). These data do not rule out the possibility that these animals may also live at greater depths or that they did so in the past. However, the absence of genera known to be restricted to deep water, and the interstratification of these marine beds with continental beds, such as the arkosic wacke with abundant plant remains, strongly suggests they were deposited in shallow water.

Subtropical climate at the time of deposition is suggested by the mollusks *Conus, Turritella, Crassatella, Anadara, Ficopsis,* and large *Venericardia* (Durham, 1950; Keen, 1963; Merriam, 1941; Smith, 1959). The dominance of *Polysyringia* over the other pelecypods in this assemblage is characteristic of living pelecypods assemblages in shallow and warm seas (Nicol and Gavenda, 1964). These mollusks support the interpretation of subtropical climate in the vicinity of Seattle during the upper Eocene based on the occurrence of the hermatypic coral *Astreopora* in these rocks (Durham, 1950), and the occurrence of subtropical plants in the type Tukwilla Formation at Steel's Crossing, one mile to the southeast (Chaney, 1940). The interpretations of Durham and Chaney have been widely cited in the review literature of Tertiary paleoclimatology (Craig, 1961; Opdyke, 1962; Schwarzbach, 1963) where this locality is regarded as one of the northernmost occurrences of subtropical climate during the upper Eocene.

Conclusions

In summary, these conclusions follow from the preceding evidence. 1) Marine basaltic wacke is interstratified with rocks identical to the Tukwilla Formation, and is therefore included in the Tukwilla. 2) The fossils in the basaltic wacke indicate a Narizian age. 3) The fossil mollusks support Chaney's (1940) and Durham's (1950) interpretation of subtropical climate in the vicinity of Seattle during the upper Eocene.

The significance of these conclusions is that these rocks are among the most easterly preserved occurrences of the marine upper Eocene in Washington and therefore refine correlations between the marine and continental section. In addition, these rocks contain some of the most northerly preserved occurrences of upper Eocene subtropical biota in North America.

Systematic Paleontology

Described here are only the single species and the single subspecies which are new. The fossil corals listed on Table 1 have been described by Durham (1942) and the other fossils have been described by Turner (1938) and Weaver (1942).

All fossils discussed in this report are deposited in the Division of Geology and Paleontology, Burke Memorial Washington State Museum, University of Washington, Seattle.

Phylum Mollusca
Class Gastropoda
Genus Epitonium Roding, 1798
Subgenus Crisposcala de Boury, 1886
Epitonium (*Crisposcala*) *wheeleri* n. sp.
Plate 1, figures 1-2

Shell small, has light broadly rounded whorls preserved with moderately deep sutures. Varices spaced one revolution apart for two revolutions and then one and one-fourth revolutions in the third. The cycle is repeated so that varices occur in pairs in direct line with another on adjacent whorls. Whorls average 14 well-developed axial ribs which are deflected just anterior to the suture. Three distinct spiral ribe cross axial ornamentation on all whorls. Two additional spiral ribs are found in interspaces of the last two whorls.
Dimensions of holotype: height 15mm, diameter 4mm; paratype: diameter 3mm.
Remarks: The spacing of varices, the numerous axial ribs and the broadly rounded whorl profile are the most distinctive features. This species resembles *E. textuvestitum* Maury (1917) except that the spiral ribs are more pronounced.
Occurrence: Tukwilla Formation: UWA 1050.
Holotype: 16917, UWA 1050, paratype: 33352, UWA 1050.

Genus Conus Linnaeus, 1758
Conus cowlitzensis Weaver subsp. *maynardensis*
n. subsp.
Plate 1, figures 9-11

The shell is small and biconical. The spire is one-third to one-half the length of the shell. There are nine whorls set with 16 to 18 nodes which are not continuous above or below the angle and which are weakly directed anteriorly. The body whorl is nearly straight sided. It is rounded slightly just below the angle and slightly concave just below the suture. The surface below the angle on the body whorl is sculptured by approximately 15 to 20 coarse, flat-topped revolving ribs which are separated by fine, flat-bottomed interspaces of one-fourth to one-sixth of the width of the rib. The surface is crossed by many fine growth lines which are worn off the holotype. The aperture is long and narrow.
Dimension of the holotype: height 22mm, diameter 8mm, angle of spire 25°.
Remarks: This new subspecies is characterized by the coarse ornamentation on the body whorl. *C. cowlitzensis* Weaver has about 40 revolving ribs while *C. cowlitzensis* subsp. *maynardensis* has 15 to 20 ribs on the body whorl.

This new subspecies was originally described by Richard C. Allison in an unpublished University of Washington masters thesis (1959).
Occurrence: Lyre Formation: UWA 217, UWA 887, UWA 892.
Tukwilla Formation: UWA 1050, UWA 3490.
Holotype: 8050, UWA 217, figured paratypes: 20314, UWA 1050, 18207, UWA 3490.

Locality Descriptions

University of Washington Localities
UWA 56—"Puget Group, Cowlitz Formation, Eocene? Oligocene? Collected on east side intersection of S. 107th and Empire Way, Duwamish, Washington." V. S. Mallory, collector, September 1952.

UWA 217—"Outcrop exposed in road cut of U.S. 101, south of Maynard, Washington on west side of Discovery Bay. NW¼, NW½ SW¼, NW¼, sec. 24, T29N, R2W." Richard Allison, collector.

UWA 229—"One hundred feet SE. of intersection of Washington State Highway and Duwamish cut off, sec. 10, T23N, R4E." D. J. Ryason, collector, January 27, 1957.

UWA 1050—NE¼, NW¼, sec. 10, T23N, R4E, Seattle South 7½′ Quadrangle. Collected by V. S. Mallory and R. McWilliams.

UWA 3420—"Collected south of intersection of S 107th and Empire Way, sec. 10, T23N, R4E." Collected by V. S. Mallory and students, spring 1963.

UWA 3421—"Collected from the Cowlitz Formation, u. Eocene. Road cut on Empire Way east of town of Duwamish and hill just north of town—approximately one mile south of Seattle." Collector, H. W. Ball, June 22, 1945.

UWA 3490—"Duwamish, Washington, Eocene." Collector, Don Frizzell, 1928.

UWA 6005—NE¼, NW¼, sec. 10, T23N, R4E, Seattle South 7½′. Quadrangle. Collected by V. S. Mallory, March 22, 1966.

University of California Localities
UCA 3207—"In a thin bed of very fossiliferous shaly sandstone on the highway three-eighths mile east of UCA 3208." Collector, J. W. Durham.

UCA 3208—"In sandstone exposed in the northwest end of low hill parallel to the Duwamish River." North side sec. 10, T23N, R4E. Collector, J. W. Durham.

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I wish to thank Professor V. S. Mallory of the University of Washington for critical reading of the manuscript. Thanks are also due Professor R. C. Allison of the University of Alaska for generously allowing me to describe *Conus cowlitzensis* subsp. *maynardensis* under my name, to Dr. George Distler of Texaco for help with the photography and to Miss Sharleen McDonald of the Burke Memorial Washington State Museum in Seattle who helped in many ways.

Literature Cited

Allison, R. C. 1959. The Geology and Megafaunal Paleontology of the Quimper Peninsula Area, Washington. Unpublished M.S. thesis, University of Washington Library. 121 p.

Arnold, R. 1909. Paleontology of the Coalinga District, Fresno and King Counties, California. U.S. Geol. Surv. Bull. 396. 173 p.

Chaney, R. W. 1940. Tertiary plants and continental history. Geol. Soc. America Bull. 51: 469-488.

Clark, B. L. 1938. Fauna from the Markley Formation (upper Eocene) on Pleasant Creek, California. Geol. Soc. America Bull. 49: 683-730.

————, and A. O. Woodford. 1927. The geology and paleontology of the type section of the Meganos Formation (lower-middle Eocene) of California. Univ. Calif. Publ. Bull. Dept. Geol. Sci. 17: 63-142.

Craig, G. Y. 1961. Evidence of climate from invertebrates. *In* Descriptive Paleoclimatology, A. E. M. Nairn, editor. New York, Inter-science Pub.

Durham, J. W. 1937. Gastropods of the family *Epitonidae* from the Mesozoic and Cenozoic rocks of the West Coast of North America, including one new species by F. E. Turner and one by R. A. Brankamp. Jour. Paleontology 11: 479-512.

————. 1942. Eocene and Oligocene coral faunas of Washington. Jour. Paleontology 16: 84-104.

————. 1944. Megafaunal zones of the Oligocene of northwestern Washington. Univ. of Calif. Publ. Bull. Dept. of Geol. Sci. 27: 101-212.

————. 1947. Corals from the Gulf of California and the north Pacafic Coast of America. Geol. Soc. America Mem. 20: 1-67.

———. 1950. Cenozoic marine climates of the Pacific Coast. Geol. Soc. America Bull. 61: 1243-1264.
Fagerstrom, S. A. 1964. Fossil communities in paleoecology, their recognition and significance. Geol. Soc. America Bull. 75: 1197-1216.
Hallam, A. 1967. The interpretation of size-frequency distribution in molluscan death assemblages. Paleontology 10: 25-42.
Hanna, M. A. 1927. An Eocene invertebrate fauna from the La Jolla quadrangle, California. Univ. Calif. Pub. Bull. Dept. Geol. Sci. 16: 247-398.
Keen, A. M. 1963. Marine Molluscan Genera of Western North America. Stanford Univ. Press. 126 p.
———, and H. Bentson. 1944. Check List of California Tertiary Mollusca. Geol. Soc. America Special Paper, no. 36. 280 p.
Livingston, V. E. 1966. Geology and Mineral Resources of the Kelso-Cathlamet Area, Cowlitz and Wahkiakum Counties, Washington. Washington Division of Mines and Geology, Bull. 54. 110 p.
Mallory, V. S. 1959. Lower Tertiary Biostratigraphy of the California Coast Ranges. Tulsa Am. Assoc., Petroleum Geologists. 416 p.
Maury, C. F. 1917. Domingo type sections and fossils. Bull. American Paleontology 5: 164-415.
McWilliams, R. G. 1965a. Paleoecologic Study of Eocene Faunule South of Seattle, Washington (abstract). Geol. Soc. America Special Paper. 265 p.
———. 1965b. Geology and Biostratigraphy of the Lake Crescent Area, Clallam County, Washington. Unpublished M.S. thesis, University of Washington Library. 166 p.
Merriam, C. W. 1941. Fossil Turritellas from the Pacific Coast Region of North America. Univ. Calif. Publ. Bull. Dept. Geol. Sci. 214 p.
Mullineaux, D. R. 1970. Geology of the Renton, Auburn, and Black Diamond Quadrangles, King County, Washington. U.S.G.S. Prof. Paper 672. 91 p.
Nicol, D., and A. P. Gavenda. 1964. Differences derived from general analysis of recent and fossil marine pelecypod faunas. Jour. Paleontology 38: 975-983.
Opdyke, N. D. 1962. Paleoclimatology and continental drift. *In* Continental Drift, Runcorn, S. K. editor. London Academic Press.
Pease, M. H., Jr., and L. Hoover, Jr. 1957. Geology of the Doty-Minot Peak Area, Washington. U.S. Geol. Surv. Oil and Gas Inv. Map OM 188.
Roberts, A. E. 1958. Geology and Coal Resources of the Toledo-Castle Rock District, Cowlitz and Lewis Counties, Washington. U.S. Geol. Surv. Bull. 1062. 71 p.
Schenck, H. G. 1926. *Cassididae* of western America. Univ. Calif. Pub. Bull. Dept. Geol. Sci. 16: 66-98.
———, and R. M. Kleinpell. 1936. Refugian stage of Pacific Coast Tertiary. Am. Assoc. Petroleum Geologists Bull. 20: 215-225.
Schwarzbach, M. 1963. Climates of the Past. New Jersey, Van Nostrand. 328 p.
Smith, A. B. 1959. Paleoecology of a molluscan fauna of the Trent Formation. Jour. Paleontology 33: 855-871.
Snavely, P. D., Jr., and H. E. Vokes. 1949. Geology of the Coastal Area from Cape Kiwanda to Cape Foulweather, Oregon. U.S. Geol. Surv. Oil and Gas Invest. Map OM 97.
———, R. D. Brown, Jr., A. E. Roberts, and W. W. Rau. 1958. Geology and Coal Resources of the Centralia-Chehalis District, Washington. U.S. Geol. Surv. Bull. 1053. 159 p.
Stewart, R. B. 1926. Gabb's California type gastropods. Proc. Acad. Nat. Sci. Phila. 78: 287-488.
———. 1930. Gabb's California Cretaceous and Tertiary Type Lamellibranchs. Acad. Nat. Sci. Phila. Special Publ. No. 3. 314 p.
———. 1956. Stratigraphic implications of some Cenozoic Foraminifera from western Oregon, pt. 2. Oligocene and upper Eocene. The Ore-Bin, Oregon Dept. Geology and Min. Ind. 18: 57-63.
Tegland, N. W. 1931. The gastropod genus *Galeodea* in the Oligocene of Washington. Univ. Calif. Publ. Bull. Dept. Geol. Sci. 19: 397-434.
Thoms, R. E. 1959. The Geology and Eocene Biostratigraphy of the Southern Quimper Peninsula Area, Washington. Unpublished M.S. thesis, University of Washington Library. 102 p.
Turner, F. E. 1938. Stratigraphy and Mollusca of the Eocene of Western Oregon. Geol. Soc. America Special Paper No. 10. 130 p.
Verastegui, P. 1953. The pelecypod genus *Venericardia* in the Paleocene and Eocene of western North America. Palaeontographica Americana 3: 112-506.
Vokes, H. E. 1939. Molluscan Faunas of the Domengine and Arroyo Hondo Formations of the California Eocene. N.Y. Acad. Sci. Ann. v. 38. 246 p.
———, P. D. Snavely, Jr., and D. A. Myers. 1951. Geology of the Southern and Southwestern Border Areas of the Willamette Valley, Oregon. U.S. Geol. Surv. Oil and Gas Invest. Map, OM 110.
———, D. A. Myers, and L. Hoover, Jr. 1954. Geology of the West-Central Border Area of the Willamette Valley, Oregon. U.S. Geol. Surv. Oil and Gas Map, OM 150.
Waldron, H. H. 1962. Geology of the Des Moines Quadrangle, Washington. U.S. Geol. Surv. Quad. Map, GQ-159.

————, B. A. Liesch, D. R. Mullineaux, and D. R. Crandell. 1962. Preliminary Geologic Map of Seattle and Vicinity, Washington. U.S. Geol. Surv. Misc. Geol. Investigations Map, I-354.
Warren, W. C., H. Norbisrath, R. M. Grivetti, and S. P. Brown. 1945. Preliminary Geologic Map and Brief Description of the Coal Fields of King County, Washington. U.S. Geol. Surv. Coal Map.
————, R. M. Grivetti, and H. Norbisrath. 1945. Geology of Northwestern Oregon West of the Willamette River and North of Latitude 45° 15′. U.S. Geol. Surv. Oil and Gas Map, OM-42.
Weaver, C. E. 1912. A Preliminary Report on the Tertiary Paleontology of Western Washington. Wash. Geol. Surv. Bull. no. 15. 80 p.
————. 1916. Tertiary Faunal Horizons of Western Washington. Univ. Wash. Publ. Geology, v. 1. 67 p.
————. 1937. Tertiary Stratigraphy of Western Washington and Northwestern Oregon. Univ. Wash. Publ. Geology, v. 4. 266 p.
————. 1942. Stratigraphy and Paleontology of the Tertiary Formations of Oregon and Washington. Univ. Wash. Publ. Geology, v. 5 (pts. 1-3). 790 p.
————, and H. Palmer. 1922. Fauna from the Eocene of Washington. Univ. Wash. Publ. Geol., v. 1. 56 p.
White, C. A. 1888. On the Puget Group of Washington Territory. Am. Jour. Sci. 136: 443-450.
————. 1889. On Invertebrate Fossils from the Pacific Coast. U.S. Geol. Surv. Bull. 51. 102 p.
Wolfe, J. A. 1968. Paleogene Biostratigraphy of Nonmarine Rocks in King County, Washington. U.S. Geol. Surv. Prof. Paper 571. 33 p.
————, H. D. Gower, and J. D. Vine. 1961. Age and correlation of the Puget Group, King County, Washington. *In* Short Papers in the Geologic and Hydrologic Sciences. U.S. Geol. Surv. Prof. Paper 424-C.

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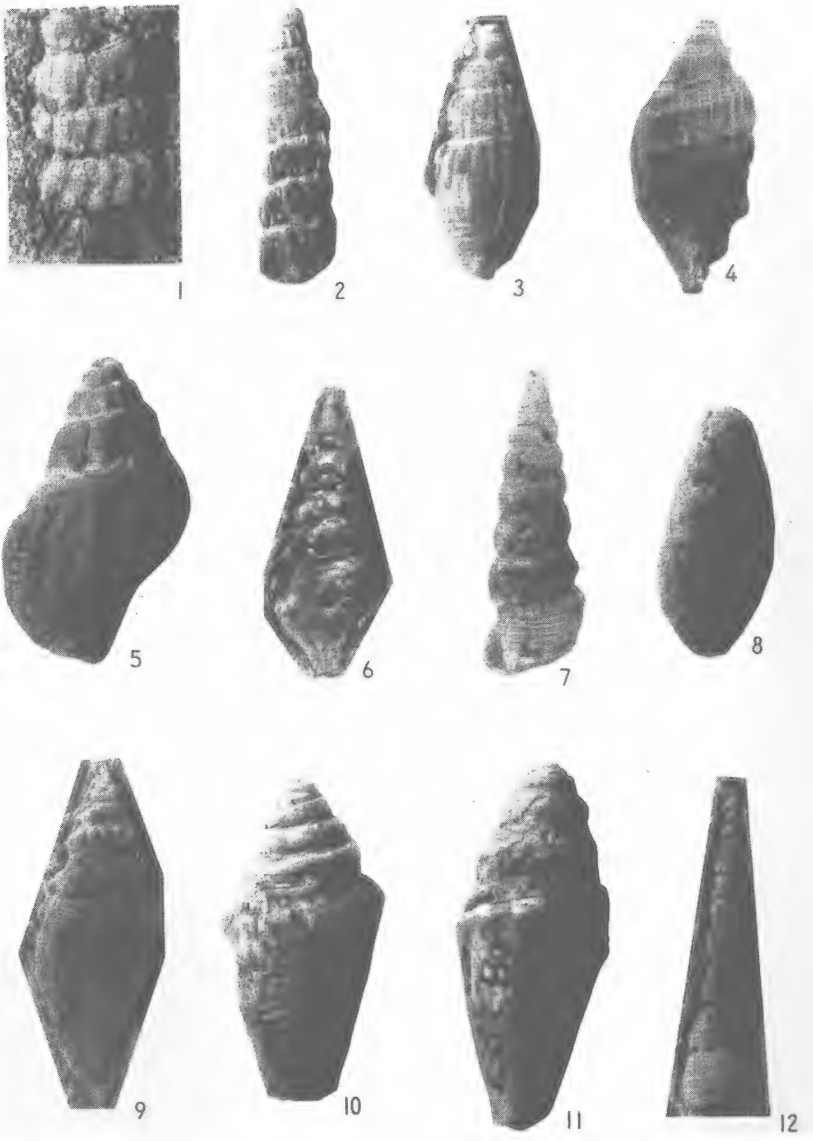

Plate 1. Figures 1-2. *Epitonium* (*Crisposcala*) *wheeleri* McWilliams 1. Paratype: 33352, UWA 1050, 7X. 2. holotype: 16917, UWA 1050, 3X. Figure 3. *Clavus fryei* (Weaver and Palmer), hypotype: 16917A, UWA 1050, 4X. Figure 4. *Ficopsis cowlitzensis* (Weaver), hypotype: 16681, UWA 1050, 3X. Figure 5. *Perse markleyensis* Clark, hypotype: 16708, UWA 1050, 4X. Figure 6. *Turricula* (*Pleurofusa*) *cowlitzensis* Weaver, hypotype: 19588, UWA 6005, 2X. Figure 7. *Turritella uvasana* Conrad, cf. *T u.* subsp. *stewarti* Merriam, hypotype: 16667, UWA 1050, 1X. Figure 8. *Scaphander costatus* (Gabb), hypotype: 18836, UWA 1050, 4X. Figures 9-11. *Conus cowlitzensis* Conrad, subsp. *maynardensis* McWilliams n. subsp., 9. holotype: 8050, UWA 217, 3X. 10. Paratype: 20314, UWA 1050, 3X. 11. Paratype: 18207, UWA 3490, 3X. Figure 12. *Turritella uvasana* Conrad, subsp. *olequahensis* Weaver and Palmer, hypotype: 13155, UWA 56, 3X.

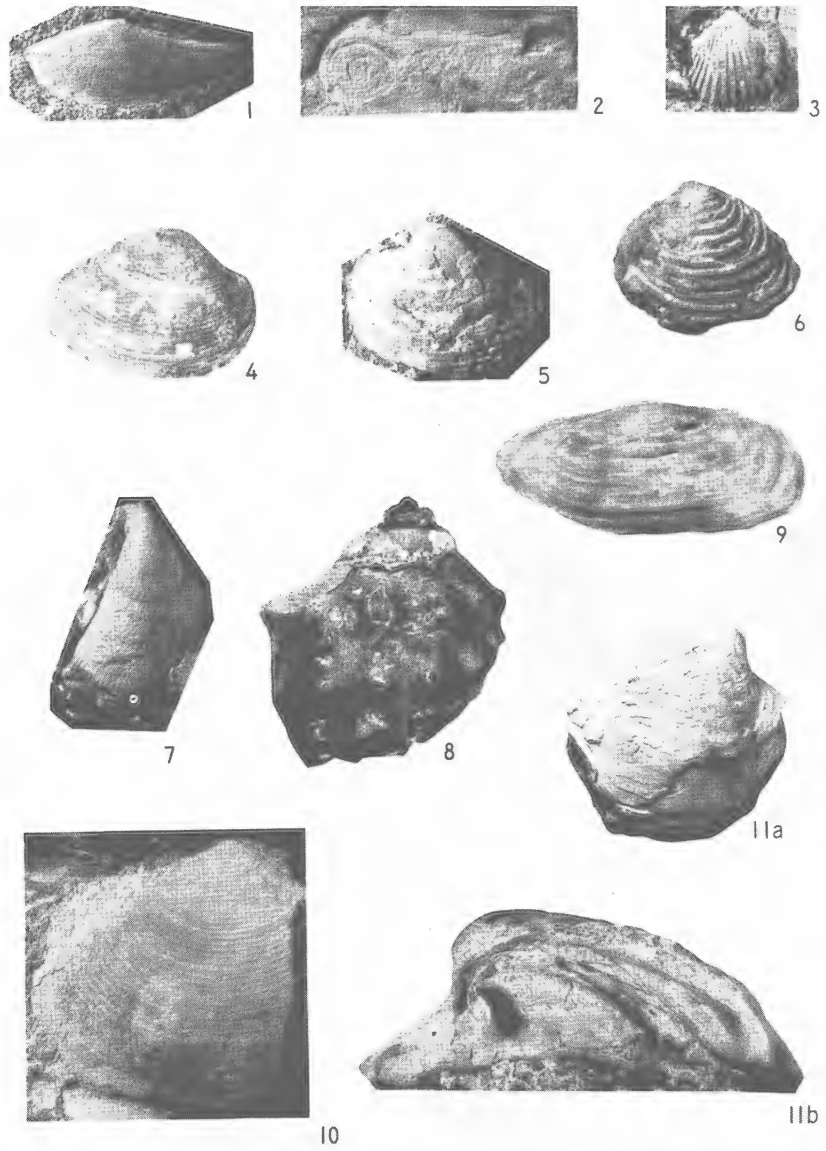

Plate 2. Figure 1. *Nuculana washingtonensis* (Weaver), hypotype: 13116, UWA 56, 3X. Figure 2. *Rotularia? tejonensis* (Arnold), hypotype: 16715, UWA 1050, 2X. Figure 3. *Venericardia* (*Pacificor*) *clarki,* Weaver and Palmer, hypotype: 16721, UWA 1050, 3X. Figure 4. *Microcallista* (*Costacallista*) *conradiana* (Gabb), hypotype: 13156, UWA 56, 2X. Figure 5. *Microcallista* (*Costacallista*) *conradiana* (Gabb) var. *meganosensis* (Clark and Woodford), hypotype: 16685, UWA 1050, 3X. Figure 6. *Crassatella lincolnensis* (Weaver), hypotype: 13147, UWA 56, 3X. Figure 7. *Septifer dichotomus,* Gabb, hypotype: 18831, UWA 1050, 2X. Figure 8. *Galeodea tri-tuberculata* (Weaver), hypotype: 18842, UWA 1050, 3X. Figure 9. *Gari columbiana* (Weaver and Palmer), hypotype: 20250, UWA 3421, 1X. Figure 10. *Tellina soledadensis* Hanna, hypotype: 13543, UWA 229, 2X. Figure 11a-b. *Venericardia* (*Pacificor*), cf. *V. lutmani* Turner. 11a. exterior view, hypotype: 20311, UWA 1050, ½X. 11b. view dentition same specimen as 10a, 1X.

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